

DIAMETRAL CHANGES IN TREE TRUNKS

BY FERDINAND W. HAASIS



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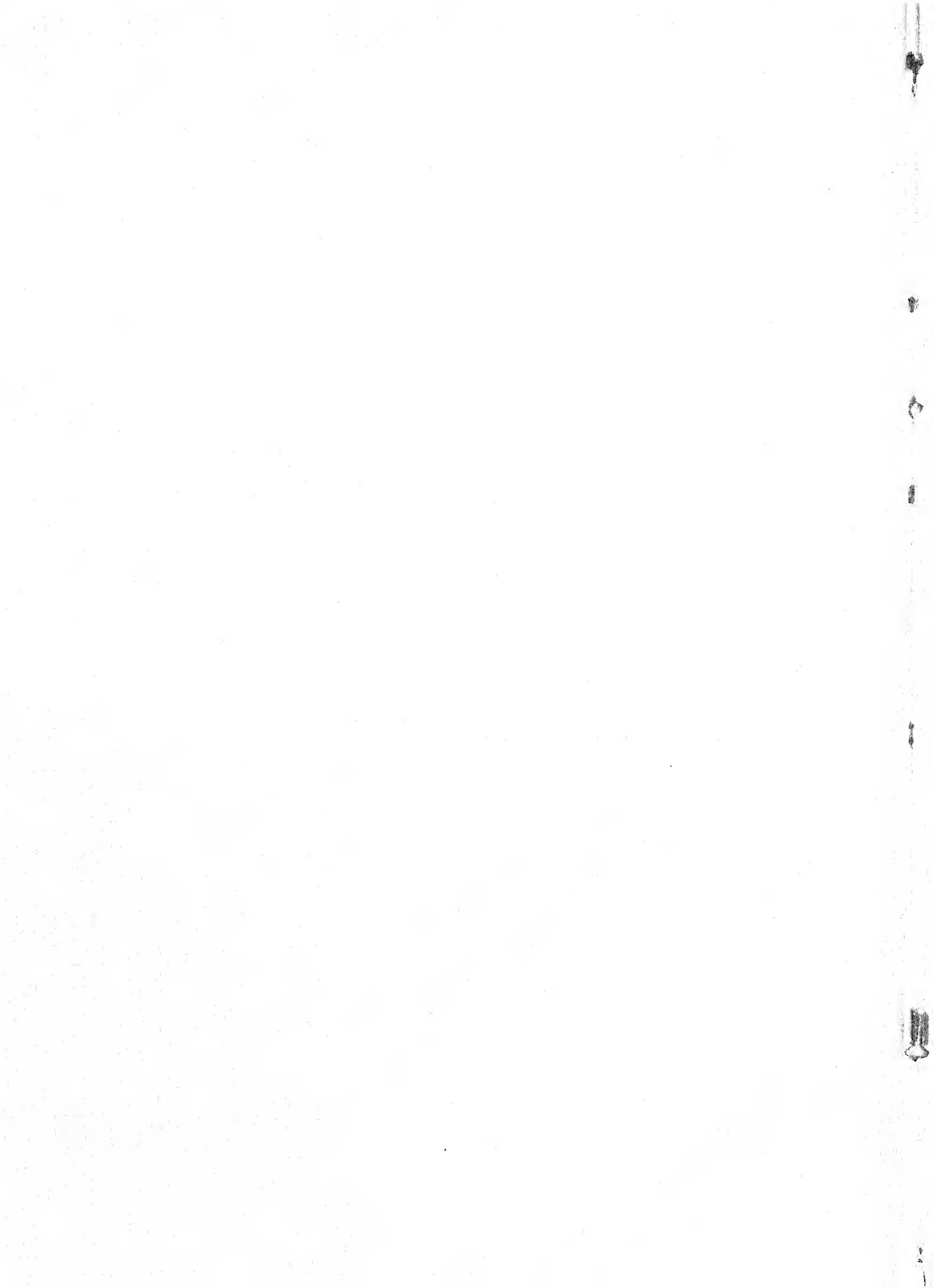


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DIAMETRAL CHANGES IN TREE TRUNKS

INTRODUCTION

HISTORICAL

That growth is not the only diametral change which takes place in plant stems has been a matter of observation for many years. As early as the last quarter of the Nineteenth Century, Kraus (1877) and Kaiser (1879) published papers in which daily diametral shrinkages in trees were referred to. These observers made their measurements with calipers (Kaiser, 1879). It was observed by Hall (1891) that monthly measurements of circumference made with a steel tape showed a certain amount of diametral shrinkage in eight deciduous trees of four species at the time of the autumnal leaf fall. Friedrich in 1905 published measurements of such shrinkages made with an automatic device (Zuwachsaufograph) employing a steel tape. In 1905 and 1910, Mrs. Spalding reported reversible changes in circumference or diameter of cactus stems. Two years later, Lloyd (1912, 61) noted that shrinkage frequently occurred during the morning in stems of tinagua (*Eriogonum nudum* Dougl.). Shortly afterward Brown (1915) reported observations of winter phloem contraction in northern white pine (*Pinus strobus* L.), attributing it to extremely cold weather.

The following year MacDougal (1916¹) published records, obtained with the auxograph, of shrinkage in both diameter and length of a cactus joint. Elsewhere (1916²) he wrote of "shrinkages or diminution of volume which have hitherto received but little attention." A couple of years later (1918¹) he presented brief generalizations on the subject of reversible variations in diameter, based on observations made upon plants of several species. With the perfection of the dendrograph in 1918 (MacDougal, 1918,² 1919,² 1921¹) it became possible to obtain with relative convenience and ease actual continuous measurements of these changes in tree trunks and there was soon available a large number of such records which showed that under certain conditions very considerable shrinkages could be expected in these woody stems. In addition to MacDougal's comprehensive reports on studies made with the aid of this instrument, several other workers have from time to time discussed various phases of such records.

In the Bibliography appended to this paper, asterisks are used to designate publications in which dendrographic results are presented. The purpose has been to list here all published original reports on the results of dendrographic experiments, whether they are specifically cited in the text or not. A list of individual trees and other plants which have formed the subjects of dendrographic studies and are mentioned in the text is given in table 18. In the text the plant numbers are indicated by italic figures.

DESCRIPTIVE

The dendrograph has been described in detail by MacDougal (1921,¹ 10-15). It will, however, help to a clearer understanding of the records upon which this report is largely based, to present here a summary of the essentials of the instrument and its manipulation. The instrument is illustrated in Plate 1.

The dendrograph consists of a rigid frame, suitably supported about a tree and carrying on one side a fixed contact rod set firmly against the tree and on the other side a movable contact rod. The latter actuates a lever to which is attached a pen. With this pen a line is traced on a record sheet carried on a revolving cylinder which is turned, by clockwork, one complete revolution a week. The instrument thus records changes in the distance between the contact points.

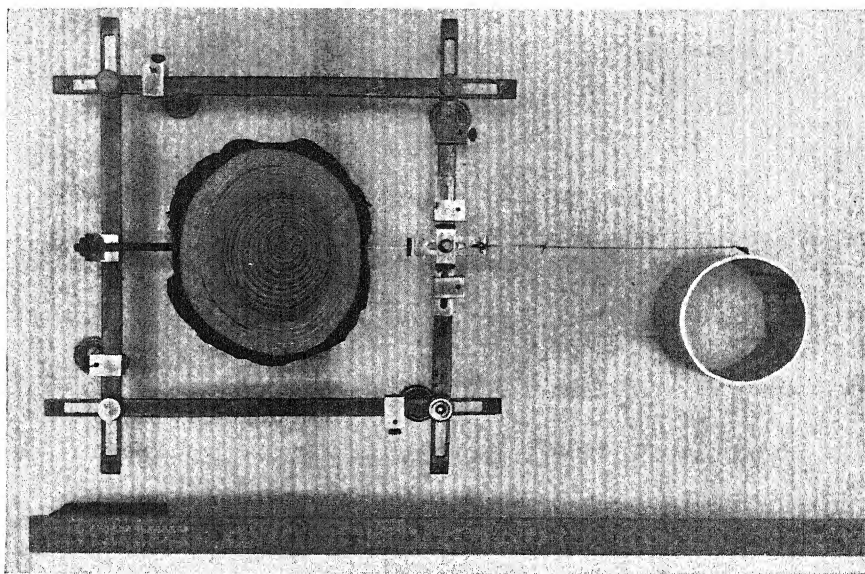
The floating frame is made up of 4, or sometimes 6, bars of some material having a low coefficient of expansion. Usually we have employed for this purpose the nickel-steel alloy Invar, or one of its modifications, i.e. Stoic, Permant, or Bario (see MacDougal, 1919,¹ 1924,¹ 37-39). On a few settings we have used rods or tubes of fused silica. This material has an even lower coefficient of expansion than the steel alloys mentioned and is lighter than the metal. It has the serious drawback, however, of being very brittle. For the most part it has been used for the members lying parallel to the diameter to be measured, on relatively large trees situated close to the laboratory headquarters. The frame members are clamped tightly together with bolts and nuts.

The fixed contact rod is of Invar, threaded to facilitate adjustment. The movable contact rods now in use are of Pyrex glass. While the coefficient of expansion of this material is somewhat greater than that of the quartz rod formerly used, it is still sufficiently low to be negligible with the lengths and with magnifications ($\times 10$ to $\times 30$) customarily used in our work. It is less brittle than the quartz. With Pyrex rods, better bearing surfaces can be prepared than with tubes, although the latter would perhaps be a trifle stronger. The end of the rod to bear against the tree is ground to a hemispherical shape; the other end, which fits in the stirrup of the pen lever, being paraboloid.

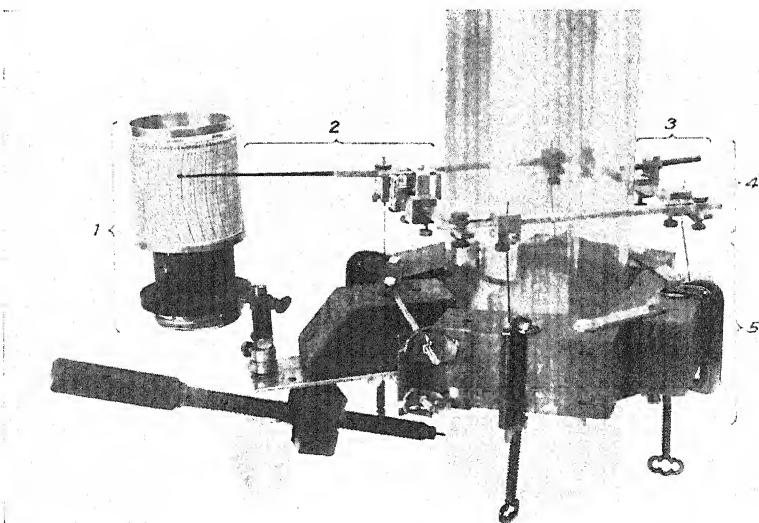
It may not be out of place here to list the coefficients of expansion for the three materials used for the frame members and contact rods. The following figures are taken from Stewart (1924), the coefficient of wrought iron being added for comparison.

<i>Material</i>	<i>Coefficient of expansion per Centigrade degree</i>
Fused quartz	0.0000004
Invar0000007
Pyrex0000032
Wrought iron0000120

For the most part, the floating frames are supported on light flexible wires (fingers) clamped to the wooden blocks of a belt which encircles the tree and also carries the recorder. The fingers are fastened at the top in brass clamps attached to the bars of the frame. In a few installations, the frame is supported from above by wires fastened to brackets of various



A—Dendrographic floating frame with contact rods, lever assembly and bar clamps about a tree section, viewed from above. Pen is shown resting against recorder cylinder. Spiral bases of wire fingers are partly visible near corners. The four Invar bars are 32 cm. long. The section is of redwood No. 11, from height of 15 dm. above ground.



B—Dendrograph set around transparent celluloid cylinder in lieu of opaque tree bole. The four bars of square frame are of Invar steel, as is also the fixed contact rod on right. Blocks of supporting belt are of redwood; metal plate under instrument block of non-rusting Allegheny Metal, and recorder cylinder and its supporting base of aluminum. Threaded wooden rod at left is used to support recorder, weight of which with aluminum cylinder is 1.2 kg. (43 oz.). Outside diameter of aluminum cylinder is 9 cm. (3½ in.). Blocks are 6.5 cm. (2½ in.) square. 1, Recorder; 2, Lever assembly; 3, Fixed contact assembly; 4, Floating frame; 5, Supporting belt.

sorts. For this we have used large bronze screws driven into the wood of the tree or, in the case of a large redwood (No. 19), shelf brackets screwed fast to the bark. For a few small plants, the dendrograph has been placed on a support beside the plant.

The recorder is customarily protected by a metal cover. On some instruments, however, we have used celluloid covers of various types; and latterly the record slips have been protected by cylindrical celluloid rain shields.

Ordinarily the distance measured is a diameter of the tree chosen before placing the instrument in position. Usually this diameter includes all or part of the bark as well as the wood and cambium. When the bark is relatively thin and smooth, the bearings are made on the intact surface. This is necessary, also, for trees such as walnut or coast live oak, whose bark contains living cells and can not be cut thin without the risk of drying out and dying at the point of injury. On comparatively large trees with rough bark where cutting is not followed by such results, it is habitual to pare the bark to a thickness of 1 or 2 mm. for each bearing. This is the usual practice when studying older individuals of redwood and most pines.

Records are sometimes lost for a number of reasons. The ink, for example, may dry or be drained away. The pen may be jolted off the sheet. Irregularities in the graphs may be caused by adjustments of the instrument.

Most of the dendrographic observations which are discussed in this paper were made at the Coastal Laboratory of the Carnegie Institution of Washington and at a number of points within 19 km. (12 mi.) to the south. The Coastal Laboratory is located at Carmel ($36^{\circ} 35' N$, $121^{\circ} 55' W$), on the west side of the Monterey Peninsula and 6 km. (4 mi.) from Monterey in Monterey County, California. To the north and east of Carmel are found low hills (200 to 300 meters high). Extending to the southeast is the Santa Lucia Range rising abruptly from the coast line, with elevations up to 1300 meters within 10 km. of the ocean. The laboratory grounds lie 1 km. from the ocean at an elevation of 20 to 40 meters. They are situated 1 km. north of Carmel Valley which is 1 km. wide and extends back into the Santa Lucias. The southern part of the grounds is located on a fixed sand dune, the northern part (the "lower garden") in a small lateral of Carmel Valley. The top of the dune is 15 to 20 meters above the lower garden. The soil in both parts is distinctly sandy, but of course much drier on the dune than in the lower garden; indeed at some times of year the water table in parts of the lower garden may be almost at the surface, as shown in open wells, and some spots are subject to occasional overflow. On the dune, a hardpan of cemented sand is found at a depth of about 1 meter, but with very irregular bounding surfaces. This hardpan may be 1 or 2 dm. in thickness. The main root layer of pine and oak apparently extends to a depth of 5 to 7 dm., but with a few as deep as 10 dm.

On the top and north slope of the dune the predominant native vegetation is a mixture of Monterey pine and coast live oak.¹ The lower garden

¹ Scientific names of most of the tree species mentioned in the text will be found in table 18 at the end of this paper. The rest are supplied in the text. The terminology is based on Sudworth (1927).

has been under cultivation in the past, but scattered trees of pine and oak are coming in here too. Arroyo willow occurs near a small stream. Among other introduced species, there are growing in the lower garden individuals of Arizona walnut, redwood, whiteleaf oak, netleaf oak (*Quercus reticulata* H.B.K.), white ash and southern (or bald) cypress.

South of Carmel, the mountains descend rather abruptly to the ocean. Here and there, however, the slopes are interrupted by narrow canyons which contain perennial streams. Although the general trend of these canyons is westerly, their courses are more or less tortuous and the inland portions are therefore sheltered from the ocean winds. Because of the steep walls there is a considerable amount of shade, especially on the south side, during a quarter or a half of the year. Dendrographic studies have been made in two such canyons, those of Palo Colorado Creek, 17 km. (11 mi.) south of Carmel, and Rocky Creek, 19 km. south ($36^{\circ} 25' N.$). The walls of Rocky Creek canyon rise 250 to 300 meters in less than 1 km. of horizontal distance. The dendrographs were on trees standing at 100 to 200 meters above sea-level. The soil of Rocky Creek canyon in the portion where the studies were made is derived chiefly from granitic rock and contains considerable quantities of rock fragments. It is much darkened by vegetable matter. On the whole, the soil occupied by the Rocky Creek redwood stands is prevailingly more moist than that of the pine stands at Carmel. On a dry slope it may, however, get down to a moisture content of 7 or 8 per cent in the dry season.

While the vegetation of the mountain slopes is largely grass and chaparral, the canyon bottoms contain stands of redwood frequently extending only a short distance above the stream. Scattered among the redwood trees are to be found bigleaf maple, tan oak (*Lithocarpus densiflora* Rehder), clumps of California laurel, and, near the streams, red alder (*Alnus rubra* Bongard). On the westerly edge of the stand, both redwood and laurel are frequently kept down to a scrubby timberline form. Farther inland the redwood may attain a diameter of 20 or 30 decimeters (5 to 10 feet) and an age of at least 600 or 700 years.

The climate of Monterey County is characterized by a rainless summer period and a rainy winter period. On the coast, overcast weather is common in the summer time. This is due to what is known locally as "high fog," a blanket of stratus cloud usually lying a few hundred meters above the ocean and varying considerably in depth with an average thickness of perhaps 400 meters (Byers, 1930, 320). At other times the fog occurs near sea-level and is called, significantly, a "dripping fog." A foggy day is likely to be cooler than a clear day, and a foggy night warmer than a clear night.

During the past 24 years, temperatures at the Coastal Laboratory have ranged from $22^{\circ} F.$ ($-6^{\circ} C.$; in January 1912 and January 1922) to $105^{\circ} F.$ ($41^{\circ} C.$; in October 1917).¹ Because of the fogginess, the summer months (June-August) are likely to be cooler than those preceding and following this period. The highest temperatures are to be expected in March-May and September-November. The shade from the steep south

¹ Erroneously given as $18^{\circ} F.$ and $101^{\circ} F.$ by Haasis (1932¹).

wall of Rocky Creek canyon makes for a comparatively cool and moist winter climate in this valley.

The average annual precipitation at the Coastal Laboratory is 17 inches (43 cm.), based on 24 years' records. This precipitation comes mostly in the form of rain, although storms of hail are occasionally experienced in winter. Heavy frost occurs at the Coastal Laboratory, but by no means every night during the winter, and mostly in the lower garden. It is perhaps a little more frequent at Rocky Creek.

The routine observations of temperature and precipitation at the Coastal Laboratory have been made on the fixed dune.

The author's indebtedness to a number of persons in the preparation of this paper is recorded, with thanks. The paper is based to a large extent upon the dendrographic records which have been accumulated during the past 15 years by Doctor D. T. MacDougal and which were made available to the writer when he became associated with the Carnegie Institution of Washington. Doctor MacDougal has, in addition, read the manuscript and offered valuable suggestions, as has also my wife. The efficient assistance of Miss Elizabeth Montgomery with compilations and in preparation of the manuscript is greatly appreciated; and likewise the help of Miss Anne Grant with the illustrating graphs. To Mr. J. C. Evenden (of the U. S. Bureau of Entomology) and to the officers of the Northern Rocky Mountain Forest and Range Experiment Station I am under obligation for the loan of original dendrograms for a western white pine, together with concurrent meteorological records.

DIURNAL FLUCTUATIONS

SPECIES FOR WHICH OBSERVED

The dendrographic records have abundantly shown that in clear weather a daily diminution and a nightly increase in bole diameter can be regarded as normal for trees of many species. Some years ago MacDougal (1921¹) stated that the trunks of all the trees so far measured showed this diurnal variation in size. These trees included individuals of 15 species located in diverse parts of the United States. Subsequent dendrographic observations by a number of workers have established the occurrence of the phenomenon in the case of several additional species of trees and other plants in various parts of the world. These species are listed in table 18. The records for bunya-bunya are not entirely consistent, but there is some indication that the diurnal fluctuation occurred in this species.

It will be seen that the phenomenon is to be expected in plants having stems of several diverse types, in gymnosperms, in monocotyledons and in both ring-porous and diffuse-porous dicotyledons.

GENERAL SIMILARITY OF PATTERN

In nearly all the species listed in table 18, the daily pattern of shrinkage and enlargement is much the same. When the trees are in a leafy condition and when the contact points of the instrument are seated on at least part of the bark, the dendrographic record in clear weather usually shows

a gradual increase in diameter up to about 8 a.m., and a somewhat more rapid diametral decrease ending at about 2 p.m. This is illustrated in figures 3, 26 and 27. A planted redwood (No. 18) growing at Carmel showed essentially the same pattern as nearby pines and as native redwoods in Rocky Creek canyon.

These observations are in general agreement with those of other workers. Kraus (1877) observed a nocturnal diametral swelling in trees which he attributed to an increase in the water content of the bark, no change in the diameter of the wood being noted. Kaiser (1879) reported a maximal diameter at morning twilight and a minimal diameter in early afternoon. He also records a secondary minimum shortly after dark. His studies were made with calipers, and apparently with no allowance for possible errors due to differences in temperature. Shortly after the development of the dendrograph, Mallock (1919) reported afternoon decreases in diameter of Douglas fir and oak trees in England. In his work, he fastened an Invar tape about the tree and observed minute changes in its length with the aid of a micrometer screw and glass reflecting surfaces forming optical interference bands. Karling's observation (1932) is that the sapodilla tree reaches its maximal diameter at 6 or 7 a.m. and its least diameter about 5 p.m.

One notable exception in pattern of diurnal fluctuations as recorded by the MacDougal dendrograph is afforded by the giant cactus. In this plant the maximal diameter is attained between 4 p.m. and midnight and the minimal in midforenoon. This is to be correlated with stomatal opening and closure (MacDougal, 1924,¹ 66-68, 86; 1924,⁴ 1932³).

The normal times of occurrence, if they may be so designated, of diametral maxima and minima in any designated region are greatly modified by weather conditions. If a rain starts before shrinkage begins in the morning, the tree may show continued increase in diameter throughout the day and the following night. If rain begins during the period of contraction, the nocturnal swelling may commence much earlier than usual. If however, a light rain is accompanied by considerable wind, shrinkage may occur even while the rain is falling.

The evaporitvity of the environment is determined by the temperature, the humidity and the rate of movement of the air, and the intensity of solar radiation (*cp.* Livingston and Haasis, 1929). The effects upon tree diameters of variations in these several factors are extremely difficult to separate from one another. An unusually windy clear day, for example, is quite likely to follow a less windy rainy day; and the shrinkages for the two successive days are not, therefore, strictly comparable. Occasionally, however, the available records are such as to indicate that the amount of shrinkage may be expected to show a very close relation to the wind velocity. This relationship is emphasized by the fact that trees enjoying varying degrees of protection from the wind show corresponding differences in response.

November 19, 1931, was clear and moderately warm, the 21st was windy but cooler; showers occurred on the 20th. The figures of table 1 illustrate differences which are probably to be ascribed to variations in wind velocity.

Pinus radiata No. 1-A, for example, shrunk 0.18 mm. more on the 21st than on the 19th, and this figure represents the increased shrinkage which appears to have been the result of the greater air movement. In the absence of precise humidity records, however, it is not certain that the moisture content of the air was the same on the two days in question.

Another example of the combined effect of wind and humidity is afforded by the records for a couple of days in April. The first of these was calm and conspicuously foggy and the maximal diameter of several trees at Carmel was attained at 8 a.m., at which time shrinkage began. On the following morning a southwesterly wind came up at about 6 o'clock, the fog becoming dissipated shortly thereafter. In spite of the fact that this wind, coming from the ocean, was presumably relatively moist, shrinkage began quite promptly after the wind's rise. For the period between 6 and 8 a.m., the two days differed in temperature by only 0.5° C.

TABLE 1—Increased diurnal shrinkage presumably due to increased wind velocity.

Tree		Shrinkage		Increased shrinkage presumably ascribable to greater air movement
		Nov. 19, 1931 (warmer)	Nov. 21, 1931 (cooler, windy)	
		mm.	mm.	mm.
<i>Pinus radiata</i>	1-A	0.27	0.45	0.18
	6	.18	.29	.11
	20	.18	.32	.14
	28	.20	.30	.10
	33	.27	.32	.05
<i>Sequoia sempervirens</i>	8	.09	.27	.18
	11	.04	.20	.16
	18	.15	.20	.05
	19	.03	.26	.23

Yet another aspect of these relations is afforded by the performance of the trees during and subsequent to an easterly (and presumably dry) wind which died down in the middle of the morning. When this wind ceased, the fact was reflected at Carmel by a decreased rate of diurnal contraction or in some cases by an actual increase in diameter.

It should be mentioned here that Phillips (1927,² 1931, 46), also, has observed that in *Olinia* and *Ocotea* in South Africa pronounced shrinkage and increase in diameter are coincident with markedly low or high humidity, respectively.

Even on a showery day there may be periods in which the evaporating power of the air is greater than at other times. On December 23, 1931, for example, nearly a quarter of an inch of rain (6 mm.) fell in showers between 8 a.m. and 4.30 p.m., and the general trend of the graphs at Carmel for this day was upward. Nevertheless several of the graphs show that there were two definite periods of contraction during the day. This is presumably attributable to the facts that sunny intervals occurred from

time to time and that the day was noticeably windy. The temperature recorded for this day shows practically no fluctuation.

In the middle of the night, too, a short windy period may result in slight shrinkages. Such a windy period occurred just before 12, on the night of November 5-6, 1931, when the wind blew for an hour or two, as is indicated by the irregular line on one of the dendrograph sheets. Several of the trees at Carmel, both leafy and leafless, showed slight shrinkages at this time. It is perhaps of significance, too, that a redwood (No. 11) standing on an exposed site at Rocky Creek and another (No. 14) some distance off began their day's shrinkage at this time and continued to decrease in diameter for several hours, although according to their usual program they would have been swelling at this time. In the case of a California laurel standing between these two, the usual nocturnal swelling failed to occur that night. Aside from this, the Rocky Creek trees apparently did not feel the effects of this wind, and several of the Carmel dendrograms as well record no nocturnal shrinkage. The dendrogram for a Monterey cypress (No. 2) at Carmel Highlands, 7 km. south of Carmel, was also normal that night. This divergence in response is presumably ascribable to the sheltered position of some of the trees. Instead of falling as usual the (Carmel) temperature remained stationary for a couple of hours before 12 on this night, but did not rise.

The general effect of fog appears to be to reduce the amount of shrinkage as contrasted with that which occurs in clear weather. Or the shrinkage may begin earlier on a clear day than on a foggy day. On July 8, 1931 (an essentially clear morning), shrinkage in the trees at Carmel began about an hour earlier than on the preceding day on which there was high fog early in the morning. This was in spite of the fact that the temperature on the night of July 7-8 went considerably lower than the night before, and at 7 to 8 a.m. the temperature on the 8th was only about 1° C. higher than on the 7th.

When the soil is dry, shrinkage may, however, occur even during foggy weather. This was exemplified in June 1931 by some of the trees on the drier sites. June 2 was an overcast day, and the following day dawned overcast, presumably after a night of high fog. Nevertheless appreciable shrinkage occurred in several trees on the 2d and their diameters were less on the night of the 2d-3d than they had been the preceding night.

A shower occurring in the middle of a clear day is almost certain to be reflected in a reduction of shrinkage or even an appreciable swelling. This is exemplified by the performance of several trees on May 17, 1933, when a light shower occurred just after noon, the temperature falling 3.5° C. The resultant modification of the dendrogram is shown for an oak (both the entire tree and the woody cylinder) in figure 5. Even a partial solar eclipse has resulted in similar interruptions of shrinkage.

On the whole, while it is a matter of great difficulty to separate the effects of each factor affecting the evaporating power of the air, it is evident from the dendrographic studies that for the most part any increase in the integrated evaporating power is reflected in an increased shrinkage

in tree trunks, and vice versa. Such effects are observed even when there is an abundant supply of soil moisture.

While in general the shrinkage pattern is much the same even for trees of diverse species, sometimes distinct differences are recorded. On a warm day in June 1931, for example, the dendrograms for two small trees 3 or 4 meters in height, a redwood (No. 18) and a whiteleaf oak (No. 2), showed a checking of shrinkage and slight diametral increase beginning at 9.30 or 10 a.m. These trees were growing in the relatively moist lower garden at the Coastal Laboratory and near larger trees of Monterey pine (Nos. 17 and 33) and Arizona walnut (Nos. 1 and 5). Although the shrinkage pattern for all these trees was much the same on preceding and subsequent days, on the day under consideration (the 24th) the dendrograms of the pines and one of the walnuts did not show the abnormality, and it was poorly marked in the other walnut. Trees on the higher and drier part of the Laboratory grounds also failed to show this type of diametral change although for a few of them, of various sizes and in varied locations, the maximal diameter for the day occurred unusually late. At Rocky Creek the redwood dendrograms (for 8 trees) showed no abnormality except for a very slight checking of shrinkage in one tree about 10 a.m.

The maximal temperature recorded in a shelter on the higher site at the Coastal Laboratory for this day was 25° C. (77° F.). This occurred about 9 a.m. Earlier in the day the minimal temperature (10° C.) had occurred at midnight, after which the temperature rose to 12° (about 1 o'clock) and then fell again to 11° (4 to 5.30 a.m.). Such temperature conditions are unusual. For the rest of the day the temperature fell rather regularly. There are no specific records of the character of the weather for June 24th, but it is unlikely that such a high temperature was reached at Carmel unless the sky was essentially cloudless.

It is possible that the abnormality in the performance of the trees is to be ascribed to irregular masses of moister air, possibly tending to be low-lying. It can well be imagined that such localized conditions favoring a reduction of transpiration would affect trees of various sizes growing on diverse sites, but would be more likely to influence the transpiration of the smaller trees on low sites than that of the taller ones or of those situated on higher ground.

AMOUNT OF DAILY FLUCTUATION

The actual amplitude of the daily fluctuation in Monterey pine may amount to as much as 1.0 mm. For redwood there has been recorded a change of 0.7 mm; and for velvet ash and ponderosa pine 1.6 mm. and 0.8 mm., respectively. In table 2 are given additional figures in which the amount of fluctuation is expressed both as a fraction of the diameter measured and as a ratio.

It will be seen from the figures of table 2 that where measurements are available for several individual trees of one species, there is a certain correspondence between the diameter of the bole and the relative amount of diurnal fluctuation. While there is some irregularity attributable to

differences in size and site, the figures for Monterey pine and for redwood indicate that in general this fluctuation is greater proportionately in the smaller trees than in the larger; and the same conclusion can be drawn, though less positively, from the figures for ponderosa pine (considering *P. ponderosa* and *P. ponderosa scopulorum* together).

Comparing trees of the same size but of varied stem structure, we find a great diversity of relations. The 5-cm. white ash (*Fraxinus*) and whiteleaf oak (*Quercus*), for example, show similar amplitude, but this is vastly different from the fluctuation in a redwood (*Sequoia*) of the same size. All three of these trees were growing in the lower garden at the

TABLE 2—Maximal recorded amount of diurnal fluctuation for trees of various sizes and species (through June 4, 1933).¹

Species and tree number	Diameter outside of bark, at contacts	Amount	Maximal diurnal fluctuation relative to diameter measured	
			Decimal fraction	Ratio
	cm.	mm.	0.0	1:
<i>Acer macrophyllum</i> 1	15	0.2	013	770
<i>Carnegiea gigantea</i> 13	40	2.6	065	155
<i>Cordyline australis</i> ?	6	0.6	100	100
<i>Cupressus macrocarpa</i> 2	16	0.5	031	325
<i>Fraxinus americana</i> 1	5	0.2	040	250
<i>F. arizonica</i>	31	1.6	052	190
<i>Juglans major</i> 5	13	0.5	038	265
<i>Parkinsonia microphylla</i> ...	10	0.2	020	500
<i>Pinus chihuahuana</i>	41	0.9	023	440
<i>P. monticola</i>	31	0.5	016	630
<i>P. ponderosa scopulorum</i> 2 ..	14	0.4	031	325
<i>P. ponderosa</i>	36	0.8	025	400
<i>P. ponderosa scopulorum</i> 1 ..	41	0.6	017	590
<i>P. radiata</i> 31	0.7	0.23	329	30
<i>P. radiata</i> 33	13	0.5	039	255
<i>P. radiata</i> 20	14	1.0	083	120
<i>P. radiata</i> 6	28	0.8	031	325
<i>P. radiata</i> 17	31	0.6	021	480
<i>P. radiata</i> 1-A	52	0.6	013	770
<i>P. radiata</i> 28	81	0.4	005	2020
<i>Pseudotsuga taxifolia</i>	36	0.6	019	530
<i>Quercus agrifolia</i> 1	22	0.3	011	870
<i>Q. agrifolia</i> 2	44	0.1	002	4400
<i>Q. hypoleuca</i> (branch) 2-A ...	1.5	0.24	160	60
<i>Q. hypoleuca</i> 2	5	0.2	040	250
<i>Salix lasiolepis</i>	14	0.2	014	720
<i>Sequoia sempervirens</i> 17	0.9	0.07	078	130
<i>S. sempervirens</i> 18	5	0.5	100	100
<i>S. sempervirens</i> 2	14	0.2	015	670
<i>S. sempervirens</i> 11	18	0.4	025	400
<i>S. sempervirens</i> 8	21	0.7	039	255
<i>S. sempervirens</i> 6	46	0.7	018	560
<i>S. sempervirens</i> 19	137	0.2	002	4400
<i>Taxodium distichum</i> 1	1.2	0.18	150	65
<i>Umbellularia californica</i> 1 ..	18	0.3	017	590

¹ The tree diameter is for the year in which the greatest fluctuation was recorded. In many of these cases, though it is not indicated, the diameter measured was less than the total tree diameter.

Coastal Laboratory. On the other hand, a 13-cm. pine experienced essentially the same maximal fluctuation as a walnut tree (*Juglans*) of the same size. These two trees, also, were growing in the lower garden. Trees of ponderosa pine (*Pinus*) and of Douglas fir (*Pseudotsuga*), on the other hand, growing near together and chosen for study because of their individual and environmental similarity, showed considerable differences in fluctuation. In other cases where different species are represented by trees of the same size, the difference in location is so great that comparisons can not be profitably made.

The greatest recorded fluctuation is for the giant cactus (*Carnegiea*), a plant whose woody cylinder is surrounded by a layer of water storage tissues (MacDougal, 1927³).

In the paragraphs immediately preceding, the discussion has been confined to the maximal daily fluctuation. From this maximum the amount may vary down to practically none at all, depending upon the character of the weather, upon moisture conditions in the soil and upon the state of the foliage.

As the soil becomes progressively drier during a period of rainless weather, the amplitude of the daily fluctuation in a Monterey pine situated on a dry site grows gradually smaller, until at the end of a protracted drouth the pen may be tracing a nearly straight line. Examples of dendrograms produced by the same tree at the end of a period of drouth and after rains had appreciably increased the soil moisture are here reproduced as figure 13. This reduction of amplitude may be explained by assuming that the water still remaining in the conducting tissue of the tree is so firmly attached to the cell walls that little or no further loss can occur, and shrinkage therefore takes place to only a limited extent, if at all. (Anticipating the discussion to be presented on a later page, it should be mentioned here that appreciable shrinkage of trees has been found to take place during a period of dry weather.)

An assumption such as that just made finds support in the records of two pine trees growing 3 dkm. apart on the grounds of the Coastal Laboratory, one of which was irrigated in the middle of the dry season in 1924. By the end of June that year, these two trees were both showing daily fluctuations which were relatively slight and of very nearly the same amplitude. Early in July water was supplied about the roots of one of these trees (No. 1), the other (No. 6) being left without irrigation. Shortly after this irrigation, the amplitude of the daily fluctuations in the irrigated tree became slightly greater than that of the control. While this divergence was comparatively small and afforded opportunity for question of the propriety of attributing the greater fluctuations of No. 1 to the irrigation, by the end of six weeks the differences were so great as to leave no further room for doubt as to the cause. In figure 1 are presented copies of the dendrograms for these two trees for a week in June 1924 and for a week in the following August. A similar relation has been observed for coast live oak, irrigated in July.

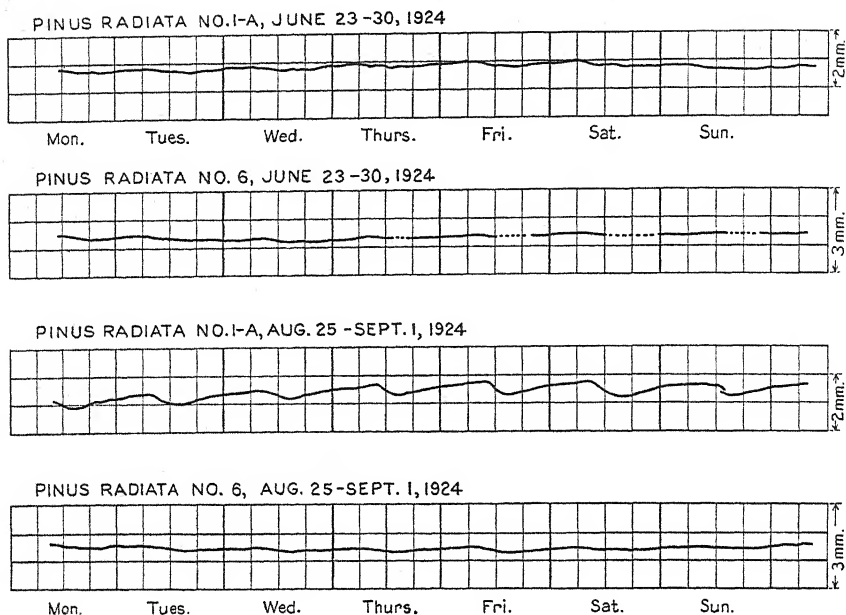


FIG. 1—Dendrographic records of two Monterey pine trees showing influence of irrigation on diurnal fluctuations. Tree No. 1 was irrigated July 3 (fig. 12); No. 6 was an unirrigated control. In this and similar graphs 6-hr. intervals are indicated by vertical lines, midnight lines being darkest. Amount of diametral change is indicated by scale at right; horizontal rulings are lines of reference; dotted graphs indicate imperfect records.

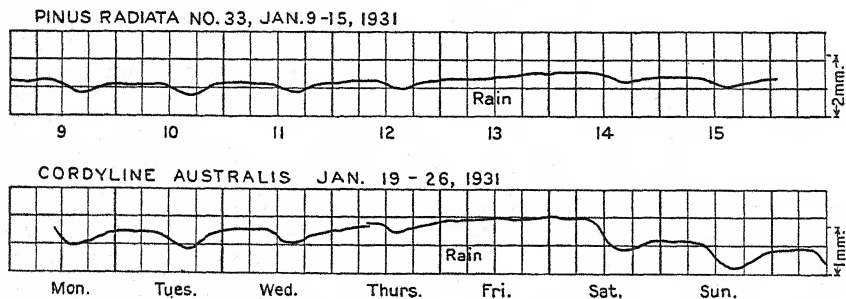


FIG. 2—Dendrographic records of a Monterey pine (*Pinus radiata*) and of a dracena (*Cordyline australis*) showing pronounced reduction of diurnal shrinkage in rainy weather. Note prompt shrinkage of the dracena in response to reduced soil moisture.

This reduction of amplitude does not occur on sites where there is a plentiful water supply. Monterey pine is occasionally found growing under such conditions, and redwood usually occupies this kind of site. Near the seaward edge of a redwood stand, however, where the trees and the ground are exposed to a great deal of wind, the plant's reaction in this respect is quite similar to that of a Monterey pine growing in dry soil.

To be compared with the reduced amplitude of diurnal fluctuation during dry weather is the essential obliteration of this fluctuation on rainy

days. Rain occurring at a time when the daily changes cover a wide range results in a marked flattening of the graph, as is illustrated in figure 2.

The immediate effects of irrigation are at times quite similar. When a maize plant (No. 1) was supplied with abundant water, the diurnal shrinkage did not always take place. It appeared that enlargement was so rapid that any tendency there might have been toward a shrinkage during the morning resulted only in a slackening of the growth-rate (fig. 3).

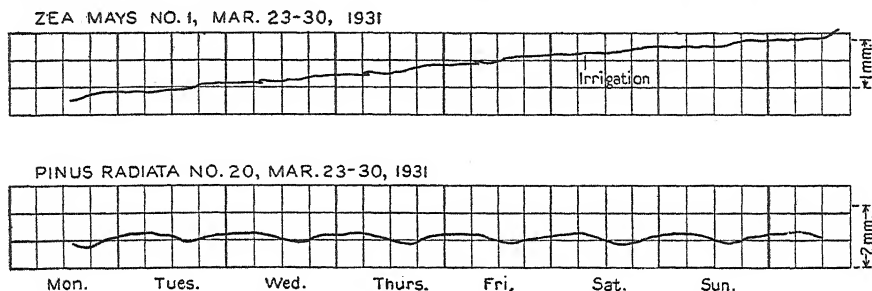


FIG. 3—Dendrograms illustrating reduced diurnal shrinkage in a fast-growing, well-watered maize plant (*Zea*) growing in greenhouse, and normal type of diurnal fluctuations in a Monterey pine tree (*Pinus*) growing outside and 1 dkm. distant. Breaks in the maize graph are due to disturbances occasioned in adjusting pen.

With less water available, diurnal shrinkage was quite definite. On this maize plant the contact points were on the outside of a cylinder made up almost or entirely of leaves and leaf bases. A corresponding effect following irrigation was observed in the case of coast live oak (No. 3). An instrument with contacts on the outside of the bark showed no diurnal shrinkage for a day or two following irrigation, and only minute contractions for a couple of days more. Another instrument, with contacts on the wood, recorded very slight shrinkages for several days following irrigation, as shown in figure 18. It will be noted that before the irrigation definite diurnal shrinkages were taking place in this tree (No. 3) and that similar contractions continued in the unirrigated control (No. 4) on the days following the date of irrigation.

In the case of some deciduous trees, it has been observed that the daily reversible variations become inappreciable during the leafless period. Lodewick (1925) reported an average daily fluctuation for white ash in New York of 1.64 mm. during the leafy period (May-September) as contrasted with 0.19 mm. for a month following the leaf fall. Such diminution has been recorded also for Arizona walnut (California), velvet ash (Arizona), sycamore (*Platanus occidentalis*, Missouri), and bigleaf maple (California). Nevertheless, it is often true that the daily fluctuation does not entirely disappear during the period of dormancy, and a slight amount may be observable even when the tree is leafless. It is of course true that the leafless period coincides very largely with the period of reduced evaporating power of the air, but it should be noted that the amplitude of daily variation in a walnut for example may remain low in the winter period, while the bole of a nearby pine shows a considerable

amount of fluctuation; the same relation holds true, though to a less marked degree, for bigleaf maple and redwood (fig. 4).

Curiously enough, California laurel which retains each suit of leaves for a number of years yields a graph almost as flat as that of bigleaf maple at the time of dormancy of the maple (fig. 4). And on the other hand, the differences between the summer and winter dendrograms of bald cypress,

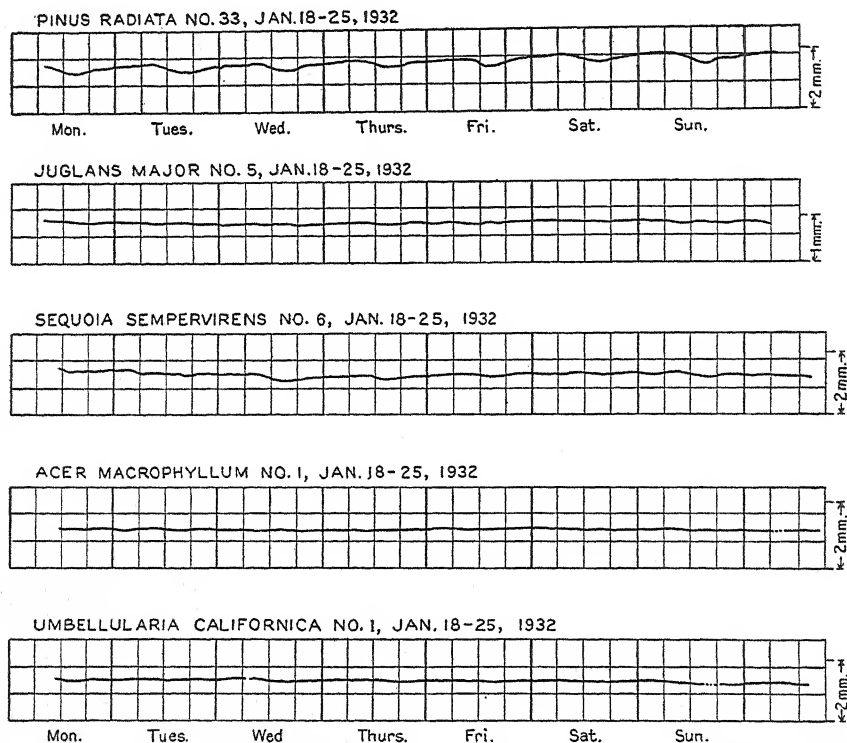


FIG. 4.—Comparison of diurnal fluctuations in deciduous broad-leaf trees during winter with those of evergreen conifers and an evergreen broad-leaf tree at same time. Walnut (*Juglans*) and maple (*Acer*) were in a leafless condition at time dendrograms were made. Pine (*Pinus*) and walnut were growing at Carmel, redwood (*Sequoia*), maple and California laurel (*Umbellularia*) at Rocky Creek, 19 km. distant. Dotted graphs indicate imperfect records.

a deciduous conifer, growing at Carmel are not so notably different as in the case of the broad-leaved deciduous trees mentioned. As a matter of fact, in this climate the bald cypress has a tendency to keep some of the old green leaves until the new ones appear. It does not, therefore, have a true dormant season comparable to that of the walnut, ash, sycamore and maple referred to above.

A small planted redwood growing at Carmel afforded an opportunity of making comparisons of its growth with that of the native Monterey pines and of the native redwoods at Rocky Creek. This redwood (No. 18) was 3 meters high and 5 cm. in diameter at the time dendrographic records were

begun. For comparison with these records there are available records for the following trees:

- A Monterey pine (No. 33) 2 dkm. distant, 9 meters high and 12 cm. in diameter;
- A redwood (No. 6) at Rocky Creek, 19 km. distant, 48 cm. in diameter, situated on a slope with north exposure;
- A redwood (No. 14) at Rocky Creek, 24 cm. in diameter, also on a north slope, and about 0.1 km. from the preceding.

The amplitude of the diurnal fluctuations in the planted tree is intermediate between that in the pines and in the Rocky Creek redwoods. On the whole it is somewhat less than in the pine, approaching more closely to that in the other redwoods, especially in the summer and autumn.

One series of dendrographic observations has been made on a tree root. The subject of this investigation was a root 8 cm. in diameter and 2 meters from the base of the trunk of a Monterey pine (No. 1) (MacDougal, 1925,¹ 34-35). Records were continued for more than 6 years. In this root (1-C) the greatest amount of diurnal shrinkage recorded was 0.15 mm., or 0.0020 of the diameter. As will be seen by reference to table 2 this is about the same, relatively, as the maximum recorded for the bole of a tree of the same species having nearly four times the diameter. The shrinkage of the root is somewhat greater than that for the bole (1-A) of the same tree on the same date, which was 0.0006 of the diameter; and indeed, it was greater than the maximum recorded for this bole (0.0013).

A few short series of studies have been made of the daily fluctuation in woody cylinders of pine, redwood, walnut and oak trees compared with that of the entire tree (*cp.* Haasis, 1933¹). In the case of a Monterey pine (No. 20) three instruments were attached to the same tree, one (20) with contacts seated on a thin layer of bark, the second (20-C) with the contacts on early formed wood of the current year's growth (about 2 mm. thick on each radius) and the third (20-B) with contact rods seated at the bottom of small holes which penetrated the bole on each side a distance equal to a quarter of the diameter of the tree. The three diameters measured were in the same vertical plane. The maximal daily variations recorded by these three instruments in 1931 were as follows:

	<i>Fraction of distance between contact points</i>
Entire tree (20).....	0.0022
Larger woody cylinder (20-C).....	.0005
Smaller woody cylinder (20-B).....	.0008

The time of occurrence of the maximal and minimal diameters as recorded by these three instruments was found to vary considerably and without any clearly ascertainable cause.

For a redwood (No. 8) there are available 7 months' records of fluctuations in a cylinder having half the diameter of the tree. In this period

the maximal relative daily variation for the inner cylinder (3-A) was 0.0004 compared with 0.0020 for the entire tree (3).

In the fall of 1931 two dendrographs were attached to a 22-cm. tree of coast live oak (No. 3) growing at Carmel. For one of these the contact rods were seated on the outside of the 4-cm. bark, while those of the other (No. 3-A) extended in shallow auger holes through the bark and some of the wood so that their inner ends rested on wood about 2 or 3 years old.

Within the first few weeks after installation there occurred diurnal shrinkages in the woody cylinder quite comparable to those in the entire tree, although on a smaller scale. Later in the season doubt arose as to the reliability of some of the records for the woody cylinder because of the closing-in of new tissues about the contact rods during the spring or summer. Toward the end of the summer of 1932, the holes were accordingly cleaned out and enlarged and the contact rods set a centimeter deeper in the wood. After that, diurnal fluctuations in the woody cylinder were inappreciable for several months.

The following April a third dendrograph (3-B) was attached to this tree, with the contact rods seated on the most recently formed wood at the bottoms of conical holes cut through the bark. This instrument was placed with the contacts intermediate in height between those of the other two instruments. The diameter measured made an angle of 80° with that including the bark and of 30° with that through only a part of the wood. This instrument likewise showed that appreciable diurnal fluctuations were occurring in the woody cylinder of the tree. After its attachment the fluctuations of the inner woody cylinder (3-A) became more marked than during the preceding few months. A comparison of records made by the three instruments is given in figure 5. The maximal diurnal shrinkages observed in this tree (through Aug. 20, 1933) were as follows:

	<i>Fraction of distance between contact points</i>
Entire tree (3).....	0.0012
Entire woody cylinder (3-B).....	.0008
Smaller woody cylinder (3-A).....	.0012

In the fall of 1930, the experiment was tried of cutting into the bark of an Arizona walnut, or nogal (No. 1), growing at Carmel, and setting the contacts of a dendrograph on a thin layer of tissue outside of the cambium. This bark was 1.5 cm. in thickness. The cambium soon died and dried up, with the result that the contact points were before long resting on the wood of the tree. About 9 months later the contacts were again set on the outside of the bark of this tree. The records obtained with these two settings can accordingly be compared with the dendrograms yielded by another instrument with contacts resting on the outside of the bark of another tree (No. 5) of the same species standing a few meters off. The dendrograms indicate that an appreciable amount of diurnal change took place in the woody cylinder of this tree, although definitely less than that occurring when both cambium and bark are included in the study (fig. 6). This observation was checked in the spring of 1933 by means of two

instruments attached to tree No. 1, one (No. 1-A) with contacts resting on the wood bared in 1930, the contact rods of the other (No. 1) being seated on the intact bark.

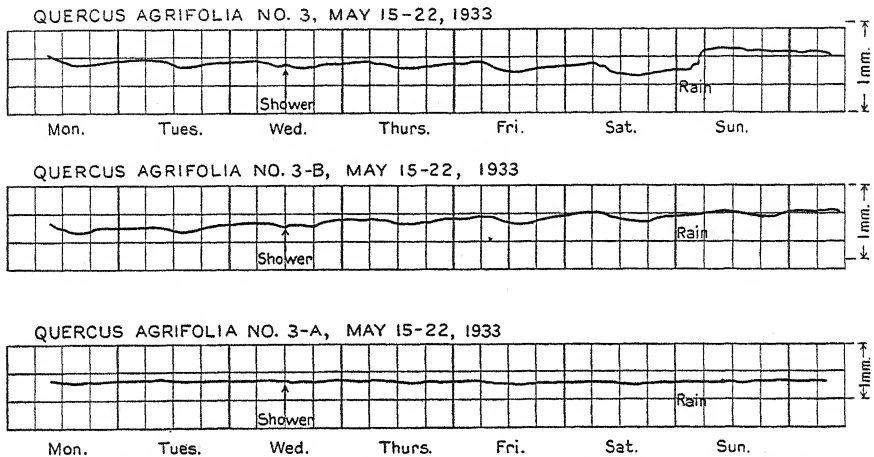


FIG. 5—Dendrographic records made by three instruments on one tree of coast live oak for same week. Contacts of No. 3 were seated on intact bark; those of No. 3-B on wood from which bark had been removed; and those of No. 3-A at bottom of holes penetrating wood to depth of 2 or 3 cm. Note occurrence of diurnal fluctuations in woody cylinder, but to much lesser extent in inner woody cylinder. Early morning rain (0.21 in., or 5 mm.) resulted in a startlingly prompt swelling of bark, and a light noon-time shower checked diurnal shrinkage. Diurnal increase of woody cylinder was less abrupt. Net diametral change experienced during week by woody cylinder was, however, greater than that of entire tree, including bark.

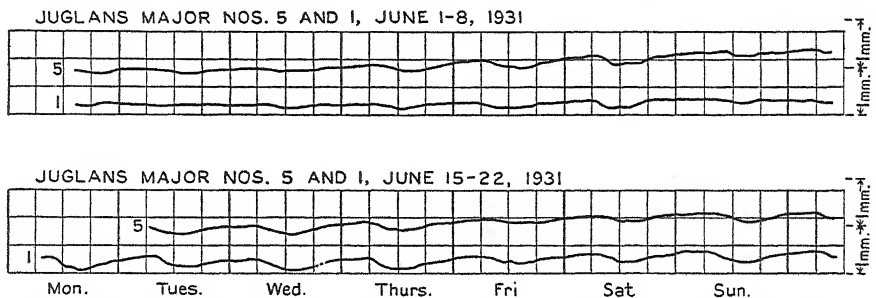


FIG. 6—Dendrographic records for Arizona walnut illustrating diurnal fluctuations in woody cylinder. On tree No. 1 dendrographic contacts were seated on bare wood during week of June 1-8. During week of June 15-22 contacts were seated on intact bark. Graphs numbered 5 are records for control tree with dendrographic contacts on intact bark. It will be seen that there was a certain amount of diurnal fluctuation in woody cylinder, although less than in entire bole including bark.

The effects on daily reversible variations of removing Monterey pine leaves by topping or defoliating and interruption of the transpiration stream by girdling have been described in some detail by MacDougal (1924,¹ 13-29; 1925,¹ 62-85). Only a brief summary of the results of these experiments will therefore be given here.

In one case mechanical girdling was performed below a dendrograph on a Monterey pine tree in May. There was no immediate appreciable change in the relative character of the dendrogram for this tree (No. 14) as compared with that for a nearby control (No. 6). The amplitude of diurnal fluctuation in the two was nearly the same. After about six weeks, however, this amplitude was definitely less in the girdled tree than in the control, and by the end of a year the girdled tree was showing practically no fluctuation, whereas the control was shrinking about 0.3 mm. each day.

Following girdling of a Monterey pine (No. 21) with hot oil in June, the diurnal fluctuations continued essentially parallel to those of a control (No. 6) for about four weeks, but then ceased rather abruptly.

The effects on diurnal fluctuations of mechanical girdling of redwoods were much the same as in the case of Monterey pine. One redwood tree (No. 15) 15 cm. in diameter was girdled in July 1924 by the removal of a

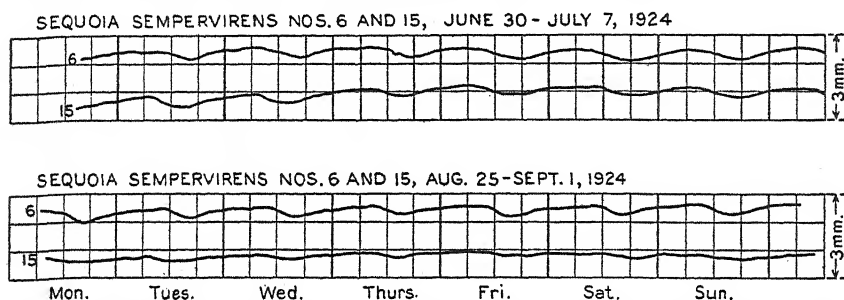


Fig. 7—Dendrograms showing effect on diurnal fluctuations of girdling a redwood tree. Tree No. 15 was girdled in July 1924 by removal of belt of bark and bast 8 cm. wide. It will be seen that whereas before girdling dendrographic records for experimental tree and its control (No. 6) were essentially parallel, after girdling amplitude of fluctuations in girdled tree was much less than in control.

belt of bark and bast 8 cm. wide. This girdling was performed below a dendrograph which had been in operation about 3 weeks. Another redwood (No. 16), not far from No. 15 and slightly larger, was girdled in August, 1928. Some strips of living tissue were unintentionally left at the time of this operation, and three years later about three-quarters of the girdled area had been covered with new wood. Girdling was accordingly repeated in July 1931 by the removal of this new tissue.

These two trees were situated at no great distance from a third redwood tree (No. 6) which was not mutilated and serves as a control. Dendrographs were operated on the experimental trees before each girdling operation and the normal relation between the performance of the experimental tree and that of the control thus established. The subsequent dendrograms obtained for the experimental trees show that each girdling was followed within two to four weeks by a marked reduction in the amplitude of daily shrinkage as compared with the amount preceding the injury (fig. 7).

Topping, also, has been performed with both Monterey pine and redwood. A small redwood (No. 9) 10 or 15 cm. in diameter was decapitated 1 meter above the dendrograph and 2 meters above the ground in July 1924. Instruments had been attached to this tree and to a nearby control (No. 8)

three months previously. By means of these, it was learned that the experimental tree for the most part showed considerably more daily shrinkage than the control. After the topping, however, the conditions were reversed and the fluctuations of the decapitated tree were much smaller than those of the control. This relation was evident the day following the operation and in general for 8 years afterward.

Topping of Monterey pine trees in May was followed at once by a marked reduction in the amplitude of daily fluctuations. This was true both when all the living branches were removed (No. 15) and when a few small ones were left on the tree (No. 10). A pine tree decapitated in March (No. 18) had been exhibiting relatively little diurnal shrinkage and the reduction after topping was less striking.

Removal of the needles from Monterey pine trees in January (No. 27), March (No. 19), August (No. 23) or October (No. 25) was followed by reduction or abolition of the diurnal fluctuations. An example of this is given in figure 8 wherein are reproduced dendrograms for two Monterey pine trees of which one (No. 19) was defoliated on March 7 and 8. It will be seen from these graphs that whereas the diurnal fluctuations of the experimental tree and its control (No. 6) were quite similar before the defoliation, the amplitude of the defoliated tree became much reduced subsequent to the operation.

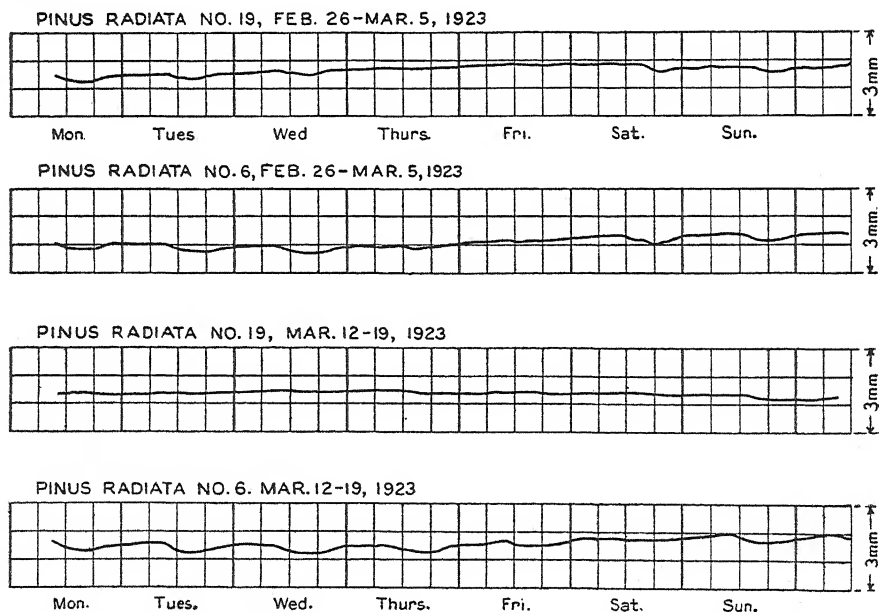


FIG. 8—Dendrographic records for two Monterey pine trees illustrating reduction of diurnal fluctuation subsequent to removal of leaves. Tree No. 19 was defoliated on March 7 and 8. Whereas there was considerable parallelism between the two records preceding defoliation date, after defoliation amplitude of diurnal fluctuations was much greater for control (No. 6) than for defoliated tree.

When the defoliation was performed at the end of May (No. 29) or early in June (No. 23), on the other hand, no marked change occurred in the

amplitude of the fluctuations. In these experiments all the mature leaves were removed. August and October defoliations, accordingly, left the tree without any leaves, whereas the trees defoliated earlier in the season still bore, after the operation, partly grown leaves of the current year's growth. (It should be noted here that the current year's leaves, though small, had already appeared at the time of the January defoliation referred to.)

Defoliation of redwood in connection with our dendrographic studies has been performed in only one instance. Whereas the leaves of Monterey pine are readily removed by pulling them directly out of the basal sheaths, those of redwood can not be thus separated without appreciable risk of seriously tearing the bark. The expedient was therefore adopted of clipping the leaves off, close to the twigs, with scissors. This procedure left the petiole on the stem and usually a short portion of the lower end of the leaf also.

The subject chosen for this experiment was a planted tree (No. 20), perhaps 10 years old, standing on a moist site on the Coastal Laboratory grounds. Defoliation was performed on March 16 to 18, 1932. Prior to this experimental work a dendrographic record had been obtained for this tree for a couple of weeks. The tree was 3 cm. in diameter at the height of the contacts, 5 dm. above ground. It stood 2 meters high and was of rather an irregular form. On February 18 the roots were below the water-level, as was evidenced by puddles of standing water on the surface of the sandy soil.

The diurnal fluctuations in this tree can be compared with those of a Monterey pine tree (No. 33) 15 cm. in diameter and standing 8 meters distant. From such a comparison it does not appear that the magnitude of the diurnal fluctuations in the redwood was materially influenced by the defoliation. The relative amount of fluctuation as between the two trees was much the same after defoliation as it had been before.

SIMILARITY TO OTHER FLUCTUATIONS DUE TO EVAPORATING POWER OF AIR

Of interest in connection with diurnal fluctuations in bole diameter are graphs published by Stocker and by White. Stocker (1929) shows the water-deficit throughout a 24-hour period for plants of various genera in Lapland, on the shores of the Baltic Sea, in Hungary, and in the Libyan Desert. These graphs are quite suggestive of the dendrograms, but complementary. The greatest deficit is shown to occur between noon and 4 p.m., and the least between midnight and 6 a.m. The deficit is greatest for the desert region and least for the Arctic.

White's (1932) studies dealt with ground-water supplies. He attributes a regular daily decline in ground-water level, observed in some localities, to the withdrawal of the water by plants. He also refers to similarly fluctuating levels of streams, especially in arid regions. (It is to be noted, however, that in dry localities, direct evaporation from the stream itself may result in pronounced fluctuations without the intervention of any plant activities.) Some of White's graphs bear a striking resemblance to dendrograms.

SEASONAL SHRINKAGE

OCCURRENCE OF SEASONAL SHRINKAGE AND
SUBSEQUENT SWELLING

In the preceding section we have dealt with periodic diminutions in diameter having a relatively short interval. In addition to these, there

TABLE 3—Seasonal shrinkage, Monterey County, California, 1931-1932.

Species and No.	Local-ity ¹	Diameter, outside of bark, at beginning of shrinkage ²	Period of shrinkage	Amount of shrinkage		
				Actual	Relative to diameter measured	
					Ratio, 1:	Fraction of distance measured
		cm.		mm.		
<i>Acer macrophyllum</i> 1....	R	17	Nov. 30, 1931 ³ - May 2, 1932...	0.8	215	0.005
<i>Juglans major</i> 5.....	C	13	July 6- Dec. 7, 1931...	1.4	95	.011
<i>Pinus radiata</i> 31.....	C	1.1	Mar. 30, 1931- Feb. 22, 1932..	1.9	5	.173
<i>P. radiata</i> 20.....	C	26	Sept. 21- Nov. 9, 1931...	0.6	365	.003
<i>P. radiata</i> 6.....	C	34	June 1- Nov. 9, 1931...	0.9	345	.003
<i>P. radiata</i> 17.....	C	47	Dec. 28, 1931- Feb. 15, 1932..	1.2	350	.003
<i>P. radiata</i> 1-4.....	C	57	Mar. 23- Nov. 2, 1931...	1.7	300	.003
<i>P. radiata</i> 28.....	C	83	June 1- Nov. 9, 1931..	1.4	505	.002
<i>Quercus hypoleuca</i> 2.....	C	5	Feb. 16- Apr. 6, 1931..	0.2	250	.004
			Aug. 3- Nov. 9, 1931...	0.5	100	.010
<i>Sequoia sempervirens</i> 17.	R	1.6	Aug. 10- Nov. 9, 1931...	0.4	40	.025
<i>S. sempervirens</i> 18.....	C	6	Sept. 28- Nov. 9, 1931...	0.2	300	.003
<i>S. sempervirens</i> 8.....	R	23	June 15- Nov. 9, 1931...	1.6	125	.008
<i>S. sempervirens</i> 14.....	R	24	Sept. 7- Nov. 9, 1931...	0.9	235	.004
<i>S. sempervirens</i> 6.....	R	48	Aug. 31, 1931- Feb. 29, 1932..	1.5	280	.004
<i>S. sempervirens</i> 7.....	R	53	Dec. 28, 1931- Feb. 15, 1932..	0.5	940	.001
<i>S. sempervirens</i> 19.....	R	137	June 15- Nov. 9, 1931...	1.3	985	.001
<i>Umbellularia californica</i> 1	R	18	Sept. 28 ⁴ - Nov. 9, 1931...	0.5	360	.003
			Dec. 28, 1931- Mar. 7, 1932..	0.9	200	.005

¹ C=Carmel, R=Rocky Creek.² In most cases the diameter between contacts was slightly smaller than the tree diameter indicated.³ Record begun Sept. 17, 1931. ⁴ Record begun Sept. 24, 1931.

are found to occur under certain conditions, other kinds of stem contraction, less abrupt than the diurnal shrinkage, but still very definite. In a later section we shall consider diametral shrinkages correlated with traumatism or with unfavorable external conditions effective for a number of years. Here we are concerned with reductions in diameter dependent upon environmental conditions obtaining for a few weeks or months. This type of diametral decrease may take place during extended periods of dry weather such as are characteristic of the summer season in Monterey County. It has been observed also during the dormant season in both evergreen and deciduous trees; and, finally, it may occur in the spring, during the period of leaf development. Such a decrease can, accordingly, be conveniently referred to as *seasonal shrinkage* and is so designated in recent papers of mine treating of the shrinkage of trees at various seasons (Haasis 1931,² 1932,¹ 1932,⁴).

Seasonal shrinkage has been observed in trees of a number of species in Monterey County. The amount which may occur is suggested by the figures of table 3. While it has taken place to a certain extent in other years, the best examples are afforded by the records for 1931-32, and it is these, therefore, which are here tabulated. From this table it will be seen that the shrinkage in the course of a few weeks may amount to as much as 0.011 of the diameter, or 0.173 in the case of a very small tree.

In figure 9 is presented in graphic form the course of diametral change for some of these trees, the amount of precipitation at Carmel during each week being also indicated. In this figure the weekly changes in diameter are shown cumulatively for each tree.

Some rather startling relations are evident from these graphs. Monterey pine No. 31, for instance, a small tree, began its summer shrinkage in early April and continued to diminish in diameter until November, with some additional subsequent shrinkage to the final minimum in February. It was not until early the following May, 13 months later, that it regained the size it had had at the commencement of the 1931 shrinkage. While this is an extreme case, several other trees which were included in our dendrographic studies behaved in a similar manner. The intervals elapsing between the beginning of shrinkage in the spring of 1931 and the occurrence of the minimal diameter in the following fall (or spring) as well as the regaining of the starting diameter in the spring of 1932 are shown in table 4.

TABLE 4—Intervals elapsing between beginning of seasonal shrinkage in trees of several species and ending of shrinkage and reattainment of beginning diameter, Monterey County, California, 1931-1932.

	Weeks between beginning of shrinkage and ending of shrinkage and reattainment of diameter	
Juglans major No. 5.....	22	42
Pinus radiata No. 1.....	32	43
Pinus radiata No. 28.....	23	48
Pinus radiata No. 31.....	47	58
Sequoia sempervirens No. 6.....	26	36
Sequoia sempervirens No. 8.....	21	41

It is not to be supposed that all trees in the region experienced seasonal shrinkage during the 17-month period covered by the figures just discussed. More vigorous individuals especially favorably situated were undoubtedly steadily increasing in diameter at this time. This was true of a young Monterey pine (No. 33) standing in moist soil not far from the walnut and oak of table 3 and figure 9. Fortnightly diametral increases for this tree for a year and a half are shown in table 10.

Another Monterey pine (No. 17) not far distant and likewise well supplied with water did not begin shrinking until late in December (as is seen in table 3). In previous years it, like No. 33, had exhibited essentially continuous growth (table 10). In 1930, however, it had suffered the loss of considerable foliage through the activities of twig-pruning insects, and was in less healthy condition than No. 33.

Other examples of seasonal shrinkage of greater or less duration will be found in figure 21. There is no need of a detailed discussion of these.

Our records show also that seasonal shrinkage may occur in the central part of a Monterey pine tree (No. 20), even though the dendrograms for the entire tree show increases (Haasis, 1933¹).

Outside of Monterey County, diametral decreases which should probably be regarded as falling in the category of seasonal shrinkage have been observed by several investigators in diverse localities. Using a number of different methods of measurement, these workers have found shrinkages occurring at various times of the year.

Besides the autumnal shrinkage in Uruguay (Hall, 1891), already referred to in this paper, another series of measurements with a steel tape has disclosed a hiemal shrinkage in Sweden (64° N.). For Scotch pine (*Pinus sylvestris* L.) Romell (1925) records a strong diametral contraction in the extreme cold of midwinter which may exceed the total increase of the preceding season. The observed linear contraction of the pines examined averaged about 0.006 of the diameter with temperatures of about -40° C. The author concludes that the phenomenon is probably due to a slight dehydration of the membranes rather than to a direct action of the temperature (p. 123). His measurements of changes in circumference were made with the steel tape resting on brass supports (pp. 121-122).

In Australia, also, according to Mr. A. D. Lindsay of the Commonwealth Bureau of Forestry (in a conversation), somewhat similar shrinkages ("decrements") have been observed in planted Monterey pine. The region where these trees are growing is without a definite dry season, and no satisfactory explanation of the shrinkage seems to have been advanced. Measurements of these trees were made monthly with calipers or tape.

Another method of observing diametral or radial changes in dimensions is by studying small chips removed from the tree at intervals (Brown, 1912; Lodewick, 1928). It was by means of such a study that Brown (1915) detected the winter phloem contraction in northern white pine, which has already been mentioned. There seems a possibility that in the trees he studied the contraction which he ascribed to extremely cold weather may have been a case of desiccation traceable to loss of water through the leaves at a time when the intake through the roots was retarded. This retardation

DIAMETRAL CHANGES IN TREE TRUNKS

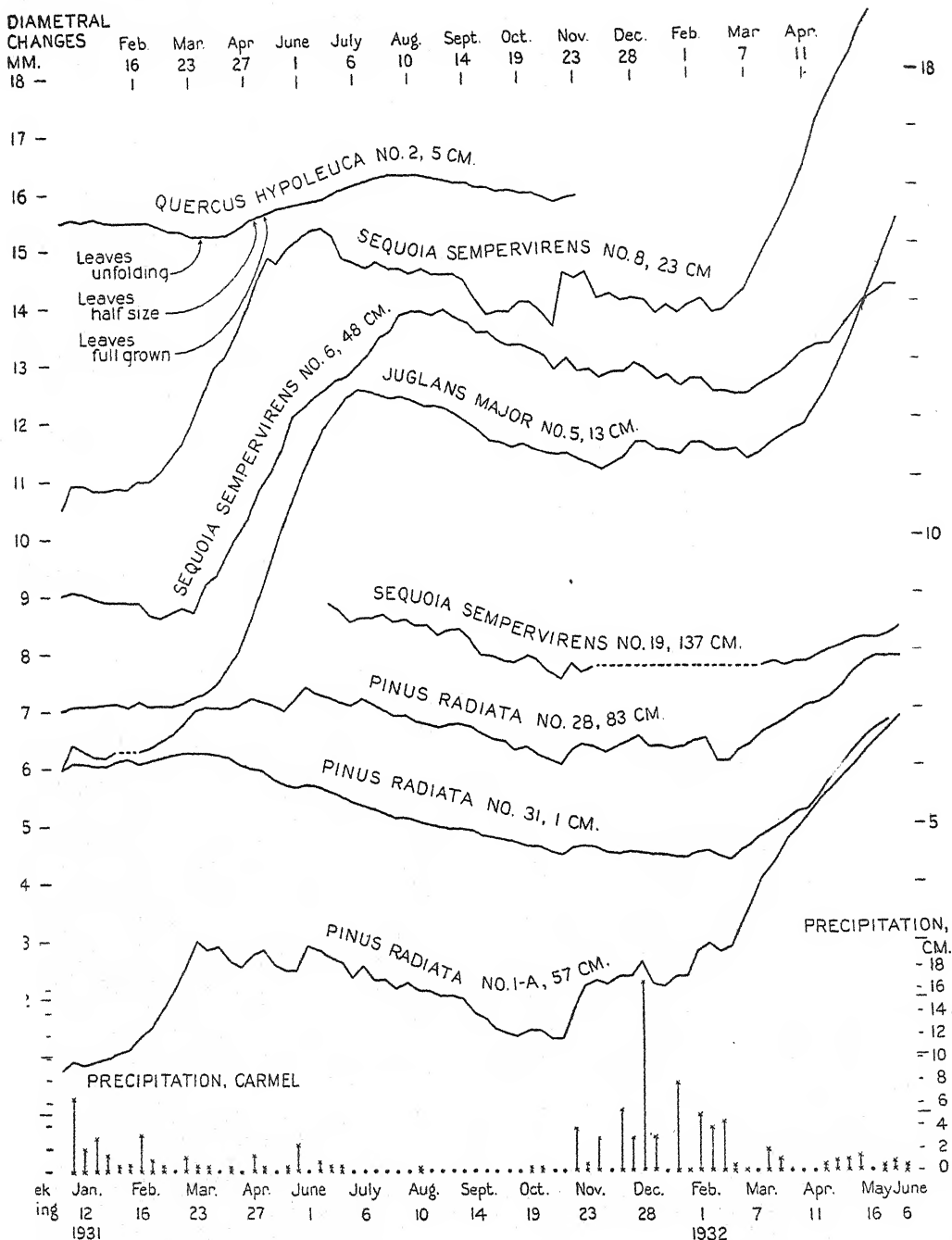


FIG. 9—Seasonal shrinkage at Carmel, California, in whiteleaf oak (*Quercus*), redwood (*Sequoia*), Arizona walnut (*Juglans*) and Monterey pine (*Pinus*) during dry spring, summer and fall of 1931, and subsequent swelling. In these graphs net weekly diametral changes are plotted cumulatively. Dotted graphs indicate periods for which dendrographic records are lacking. Weekly precipitation figures are plotted for comparison with dendrographic records, dots indicating no rainfall for the week single measurements were made. Diameter of tree at beginning of record.

might be incident to actual freezing of the soil about the roots. In other words this contraction may, perhaps, be regarded as a type of seasonal shrinkage, the result of excess of water loss over water intake, as in other cases of seasonal shrinkage.

With the same method Chalk (1930) observed for trees of two species of ash (*Fraxinus excelsior* L. and *F. oxycarpa* Willd.) and Douglas fir, in England, that after the cessation of growth in August or September there appeared to be in September and October an actual reduction in *width* of the *ring* formed during the current season. For this he was unable to offer any explanation (p. 18, and fig. 1, p. 13.)

Morikawa (1925), who used both direct measurement and anatomical observations in studying two species of pine, noted that growth in thickness of the current year's twig was temporarily suppressed during the time when the winter buds were being formed.

The dendrographic studies outside of Monterey County afford a few instances of seasonal shrinkage. MacDougal, for example, has reported dendrographic records of diametral shrinkage for periods of a few days or up to three weeks in trees of various species (1921,¹ 28-35; 1924,¹ 11; 1930,⁴ 342-343). In one case a Chihuahua pine in Pima County, Arizona, in three weeks lost by shrinkage about three-fourths of the amount it had gained during the preceding six weeks. This is probably an example of seasonal shrinkage for a short period. Pearson, who also worked in Arizona, in Coconino County, writes of shrinkage during dry weather in trees of western yellow pine (1924). In New York Lodewick noted diametral shrinkages in white ash taking place in both June and October (1925).

Recent observations on sapodilla in British Honduras have afforded another excellent example of seasonal shrinkage. Karling (1932) describes this in the following words: "The trunk begins to increase in diameter during the latter part of May and early June at the beginning of the rainy season and reaches its maximum in December. As the dry season begins in January a precipitous [reduction] in diameter occurs, which continues to a minimum in April and May."

In some other of the available dendrographic records for trees of a number of species in various parts of the United States, seasonal shrinkage is suggested, but the evidence is inconclusive. There seems no reason for believing, however, that it would not be found to occur under certain environmental conditions. It would be expected in trees which retain their leaves during a period when water entered the roots with difficulty. A condition of this sort might be due to dryness of the soil, as in the typical summer period in Monterey County, or to the fact that the soil moisture was frozen.

Seasonal shrinkage should also be looked for in deciduous trees during the leafless period. As we have seen, it has been observed for several deciduous species during a cold dormant period. It is probable that comparable studies of leafless trees in a dry dormant season would disclose similar shrinkages. Besides the shrinkage during the dormant period of deciduous trees, dendrographic records also show winter-time shrinkages for the evergreen redwood and California laurel, in spite of soil moisture contents which are obviously sufficient for growth.

Decreases in diameter during the period of leaf development have been observed for big-leaf maple (No. 1) and for two exotic deciduous trees, white ash (No. 1) and bald cypress (No. 1) at Carmel.

Occasionally the autumnal shrinkage is followed by hiemal or hiemal-vernal shrinkage without an interval of rehydration. This may happen with evergreens as well as with deciduous trees. An example of this is afforded by redwood No. 6 in 1931-32 (fig. 9).

The response of two other plants to diminishing soil moisture should be mentioned here. These are dracena and giant cactus. A plant of the former growing at Carmel showed very prompt shrinkage in the absence of rain or irrigation (figs. 2, 10). The giant cactus is very sensitive to changes in water supply, fluctuating violently in diameter, as can be seen in figure 11. This plant (No. 33), about 2 meters high, was growing at Tucson, Arizona, in its native climate. A shrinkage has been recorded for it (in the spring of 1931) of nearly 16 mm. within a space of 4 weeks.

Attention seems to have been drawn to seasonal shrinkage in Monterey County mainly by an autumnal or winter swelling whose cause was not clear. MacDougal, for instance, speaks of slight enlargement in late fall or early winter which seemed to be characteristic of Monterey pine at Carmel (1924,¹ 10).

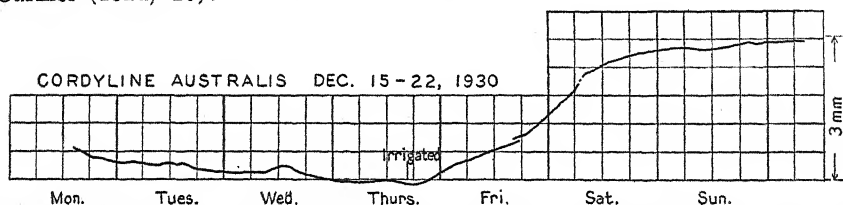


FIG. 10—Dendrogram showing response of dracena to irrigation following period of shrinkage incident to reduced soil moisture.

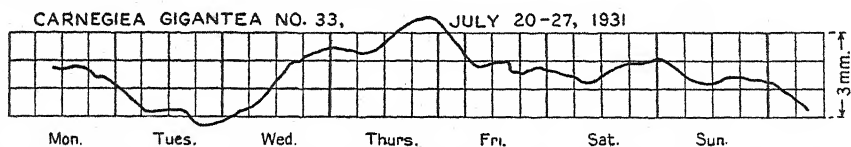


FIG. 11—Dendrogram illustrating violent fluctuations in diameter of a tree cactus; Tucson, Arizona.

It appears now that this diametral increase should probably be ascribed mainly to rehydration of tissues which have been desiccated during a preceding period of dry weather. As a dry season advances, the water supply in the soil is progressively depleted. In the sandy soil at the Coastal Laboratory the moisture content has been known to become reduced to 3 or 4 per cent (based on the dry weight of the soil) at a depth of 30 to 50 cm. During such a time conditions continue favorable for loss of water through the leaves of the tree. It seems, moreover, that the roots can not take in moisture from the soil fast enough at night to make up for the losses during the day. Consequently, the tree tends to be smaller each night than it was the night before. When such conditions obtain over a period of many weeks, we witness one type of the phenomenon which I have denominated *seasonal shrinkage*.

It is not thinkable that this process can continue indefinitely. The dying of established trees during periods of extreme drouth is indeed a not unknown phenomenon.¹ When a site is subjected too frequently to periods conducive to seasonal shrinkage of the trees of a given species, we would not of course expect to find this species established there.

The seasonal shrinkage of Monterey pines during the dry year of 1931 (which is shown graphically in figure 9) may be regarded either as one period of unusual length and interrupted by periods of rehydration (or growth), or as two periods, the one ending in mid May, the other in November. Whichever way we look upon it, the fact remains that in this spring when the soil was unusually dry, shrinkage of the trees occurred which ordinarily is to be expected in the dry autumnal season. The heat conditions at that time were undoubtedly favorable for tree growth, judging by the cambial temperatures (see section on Diametral Increases) and by the fact that shrinkage did not occur in trees with an obviously more plentiful water supply than that enjoyed by those in which shrinkage took place.

CONDITIONS AFFECTING SHRINKAGE AND REHYDRATION

When water again becomes available to the roots of a tree which has suffered dry-season shrinkage, enlargement ensues. This is evidenced when

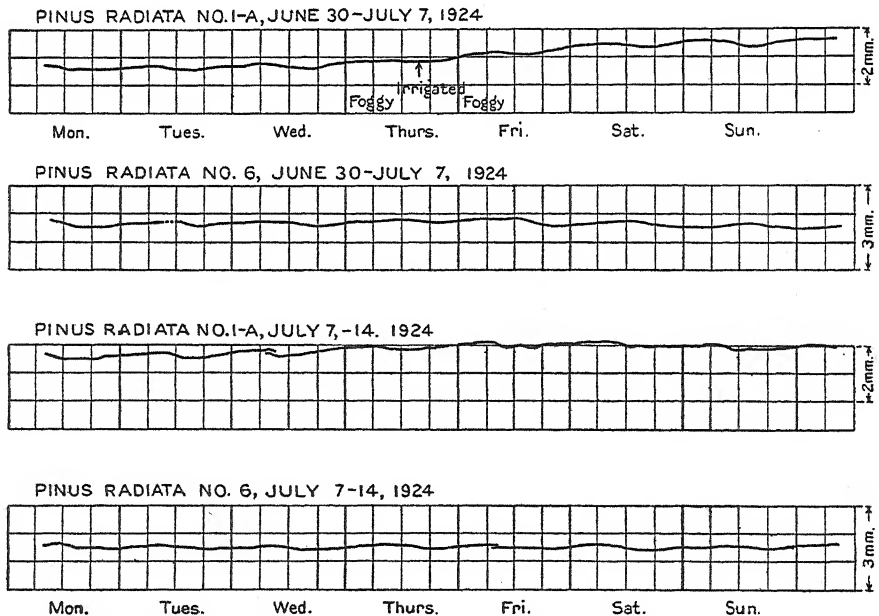


FIG. 12—Dendrograms illustrating enlargement in Monterey pine following irrigation. Dotted graph indicates imperfect record; breaks in graphs are due to disturbances of instrument.

a tree is irrigated after a period of dry weather (figs. 12, 18). Similarly, enlargement is to be expected as a result of rain, as is illustrated in figures 5 and 13. There is a possibility that enlargement after rain may be due in part to swelling of the bark as a result of the accession of moisture to

¹ See, for example: Meinecke (1925), Phillips (1931, 51), Hursh and Haasis (1931).

the outside. This matter will be taken up in more detail in a later section. The reduction of evaporation, too, commonly concurrent with rainy weather, would of course favor enlargement rather than shrinkage. In view of the observed effects of irrigation, however, it seems reasonable to suppose that an appreciable amount of the diametral swelling which follows rain is to be ascribed to an increase in the amount of water available at the absorbing surfaces of the roots.

The conditions influencing seasonal shrinkage during dry weather and subsequent swelling are very much the same as those affecting diurnal fluctuations. Indeed, the two may well be looked upon simply as different phases of one general phenomenon. When the evaporating power of the air is great, seasonal shrinkage is relatively rapid. Trees with a plentiful water supply do not suffer the dry-weather seasonal shrinkage.

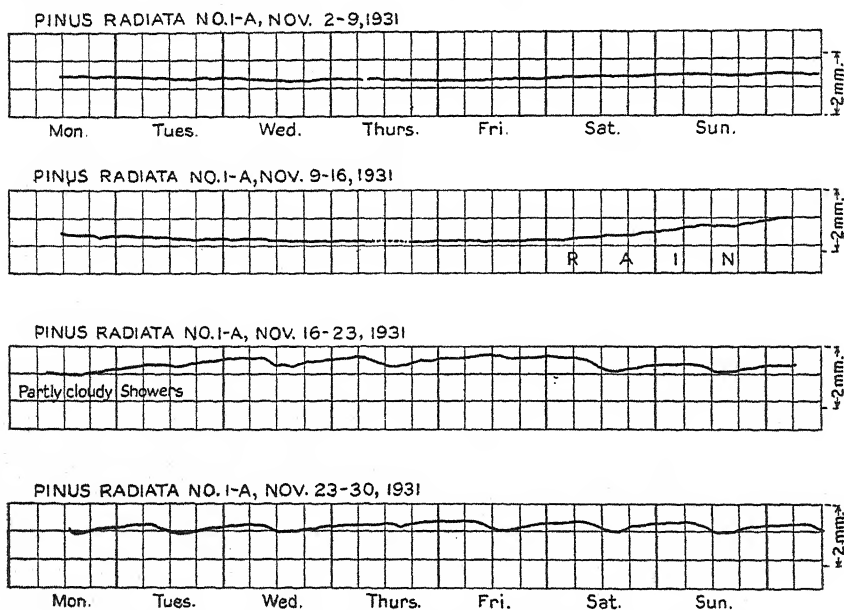


FIG. 13—Dendrographic records of tree of Monterey pine showing reduced diurnal fluctuations at end of period of drouth, diametral increase as result of rain, and increased diurnal fluctuations following rain. Precipitation for 48-hour period ending at 8 a.m., Nov. 15 amounted to 34 mm. (1.32 in.). Dotted graph indicates imperfect record.

The æstivo-autumnal shrinkage is difficult to separate from the hiemal type. At times, indeed, the two seem to merge (fig. 9). Nevertheless it appears likely that the former is determined by lack of soil moisture, whereas the latter is dependent upon the prevalence of weather too cold for growth and is allied to the winter shrinkages occurring in leafless deciduous trees (figs. 9, 14, 15). The net result of the winter shrinkage is the same as in the case of the other kinds of shrinkage which we have considered. The general relation obtaining has been expressed by MacDougal, referring to daily reversible variations, in the following words: "contraction or shrinkage is an invariable attendant of lessened water-balance due to an excess of transpiration over water supplied" (1925, 3).

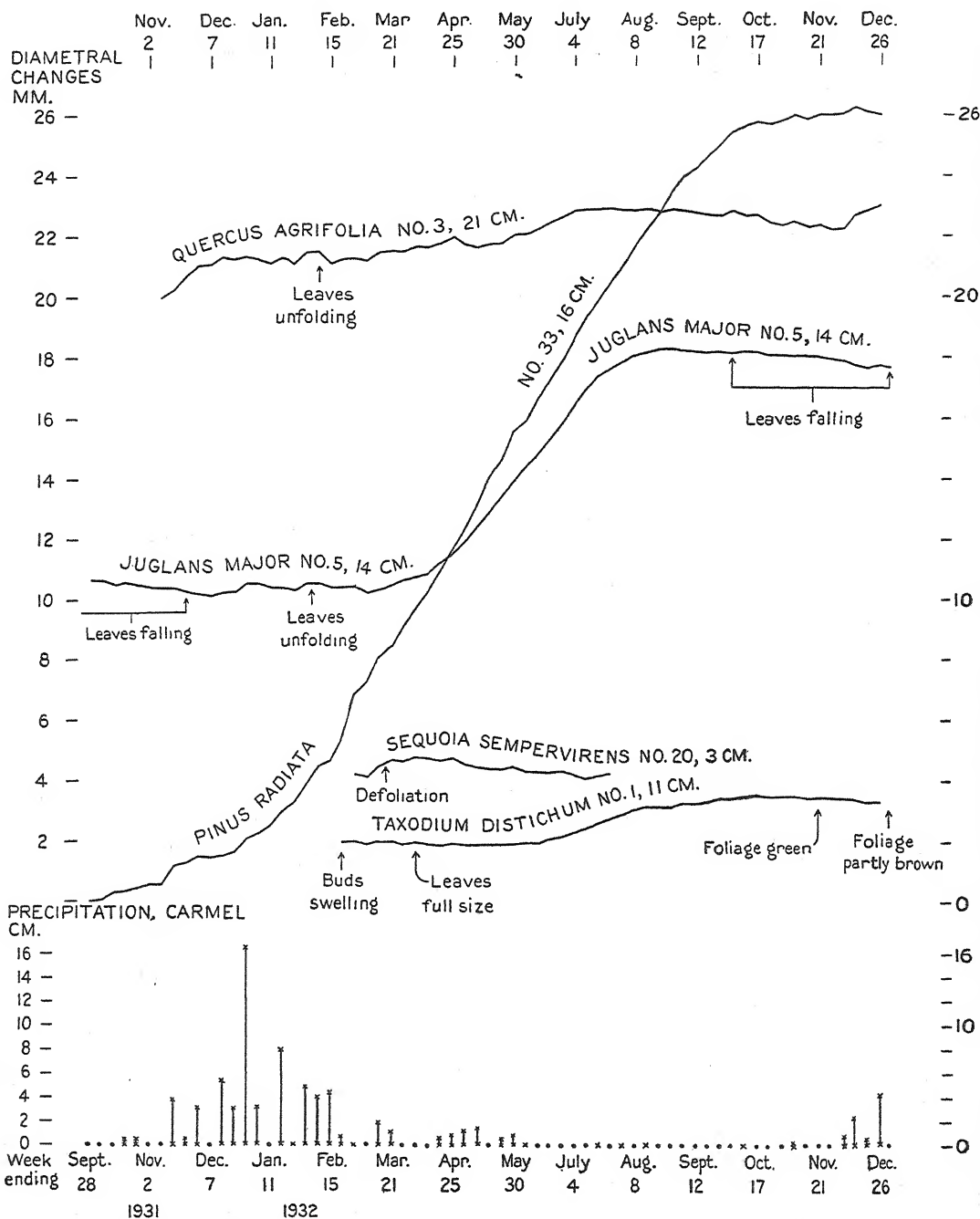


FIG. 14—Seasonal program of diametral changes for deciduous and evergreen trees, 1931-32; Carmel. Dots at foot of figure indicate no precipitation for week, single crosses a small amount.

DIAMETRAL CHANGES IN TREE TRUNKS

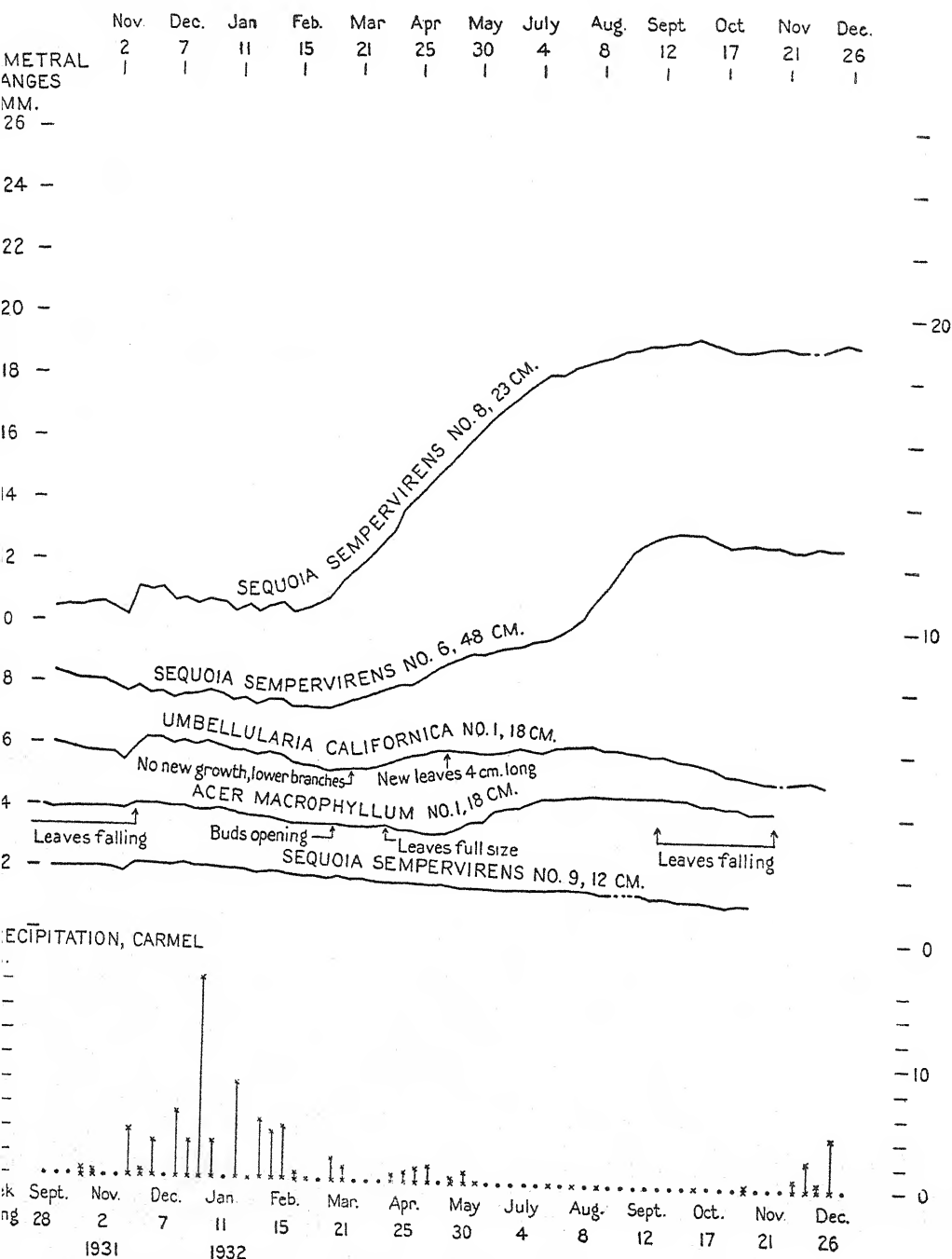


FIG. 15—Seasonal program of diametral changes for deciduous and evergreen trees, 1931-32; Rocky Creek. Dotted graphs indicate missing records. Dots at foot of figure signify no precipitation for week, single crosses a small amount.

Winter shrinkage of evergreen trees has been found to be more common at Rocky Creek than at Carmel. This is undoubtedly ascribable to the fact that the topographic conditions favor prevailingly cooler winter temperatures at Rocky Creek than at Carmel.

Spring shrinkages may be occasioned by the removal from the stem of stored food products which are used in the development of elongating shoots and enlarging leaves (*cp.* Pfeffer, 1903, 13). They may also be attributable in part to the progressively increasing transpiration incident to increasing expanse of leaf surface, as has been suggested by Weaver and Mogensen (1919).

Judging by Morikawa's (1925) observations it seems possible that withdrawal of food materials in formation of buds may account for a small amount of summer or autumnal shrinkage. It is by no means certain, however, that this could be detected far down in the bole.

It is to be noted that swelling frequently occurs during the night, even when a tree is undergoing definite shrinkage from day to day (fig. 16). When fog intervenes to reduce the evaporating power of the air, shrinkage may be temporarily checked or the movement even reversed (fig. 17).

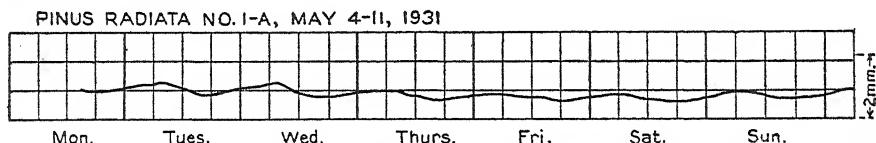


FIG. 16—Dendrographic record of Monterey pine showing nocturnal expansion during period of seasonal shrinkage.

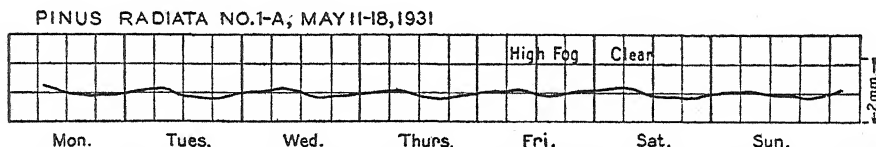


FIG. 17—Dendrographic record for Monterey pine tree showing checking of shrinkage by high atmospheric humidity.

Exceptions to this response are afforded by trees growing on two quite diverse sites. One very small Monterey pine tree (No. 31) on a dry site continued to shrink even during a notably foggy night in the middle of a prevailingly rainless period. To be contrasted with this effect is the response of other trees, pines and redwoods, better supplied with moisture and increasing in diameter from day to day rather than decreasing, which showed no marked change in daily program on this foggy night. In the one case it would seem that the roots of the small tree were not extensive enough to enable it to take full advantage of the reduced evaporating power of the air. In the other, it is to be supposed that even on a clear night the trees were already taking in all the moisture of which they were capable and so a reduction of the evaporating power of the air was of no significance to them.

With low soil moisture contents, the difficulty of the tree's extracting water from the soil is, of course, very great. We can envisage a state of affairs

where the available water in the soil is so deficient that only an exceedingly small amount of nocturnal rehydration can take place even when the evaporating power of the air is low.

The rate of dry-season shrinkage is obviously a function of both the water-supplying power of the soil and the evaporating power of the air. When water is available only in excessively small amounts, while transpiration continues active each day, shrinkage must ensue. Eventually, it appears, the tree's moisture becomes depleted to so great an extent that there is little available for daily losses, even when the evaporating power of the air is great. It is under such conditions that the diurnal shrinkage is reduced to a minimum, as elucidated earlier in this paper.

TRAUMATIC AND PROLONGED SHRINKAGE

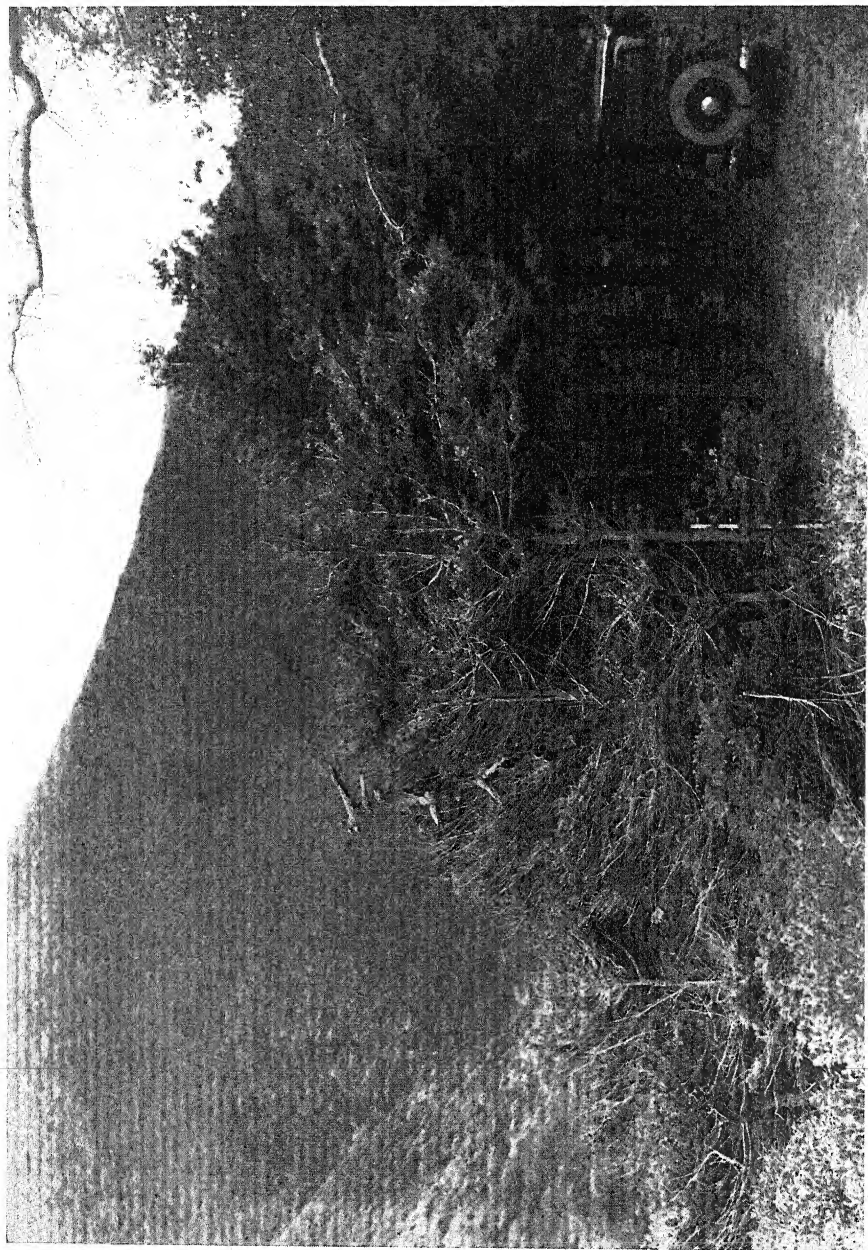
Shrinkages of greater or less duration have been observed to follow traumatism of various sorts. Other protracted shrinkages are to be ascribed to the prolonged continuance of unfavorable external conditions. Both types of diametral decrease are obviously due to some interference with the normal course of development of the tree. It is because of this close relationship that they are here discussed together.

SHORT-PERIOD SHRINKAGE

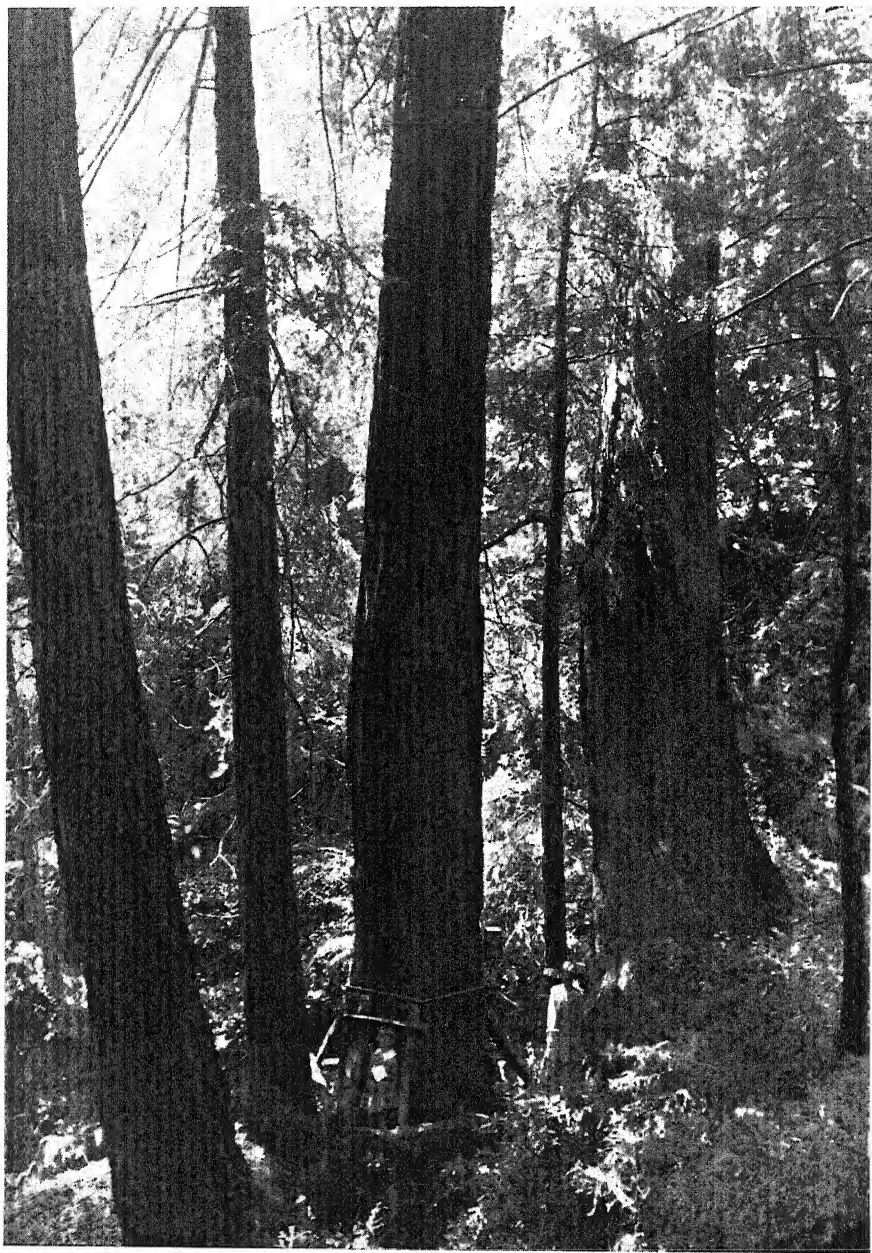
MacDougal (1924,¹ 21; 1925,¹ 69, 72, 77-78) has recorded a few examples of dendrographic records of shrinkage in Monterey pine trees following decapitation or defoliation. Shrinkage apparently due to the traumatism began in one tree (No. 15) within 2 months after topping and continued for the next 3 months, when the dendrographic record was stopped. In another case (No. 10) shrinkage was noted in a tree two years after topping. This appeared to be correlated with death of the phloem on one side of the tree. Indeed shrinkage for periods of a few weeks had begun to occur in this tree within two months after decapitation; and these reductions in diameter were not paralleled in a nearby control tree (No. 6). Another tree (No. 25) which died subsequent to defoliation showed shrinkage immediately after removal of the leaves in October, and there were very few weeks in which diametral increases occurred up to the middle of the following May. Still a third pine tree (No. 27), defoliated in January, began to contract in a couple of weeks and was shrinking quite definitely by the first of May. In this case, too, death followed the defoliation.

Standing in contrast with the above cited examples is the history of another Monterey pine growing on a moist site. Following decapitation no immediate nor marked shrinkage occurred in this tree (No. 16), but for 7 years after the topping operation it failed to grow as well as its control (No. 17) 2 meters distant. It is conceivable that if this tree had had a less plentiful water supply, it, too, might have experienced a prolonged diminution of diameter.

When the leaves were removed in mid-March from a small redwood (No. 20) growing at Carmel, diametral increase, which had already begun, practically ceased, and considerable shrinkage took place during the succeeding 3 months. In this period an essentially complete suit of new leaves was



Stand of wind-dwarfed redwoods, Rocky Creek, Monterey County, California. Tree by meter stick in foreground is 3 meters high, 7 cm. in diameter, and at least 32 years old (1933). No. 11 stood 6 meters from this tree. In background is chaparral-covered north wall of canyon.



Stand of mature redwoods, Rocky Creek, Monterey County, California.
Erect tree in center, with figures at base, is No. 19.

developing. The course of diametral changes in this tree is shown in figure 14, where are also given the corresponding seasonal performance of an unmutilated evergreen conifer, of a deciduous conifer, and of a deciduous angiosperm. These four trees were all growing within 25 meters of one another.

LONG-PERIOD SHRINKAGE

Other examples of shrinkage not attended by death of the tree and extending over a longer period of time are afforded by two redwoods growing at Rocky Creek. One of these trees (No. 11) was situated near the edge of the redwood stand, where the wind movement tends to keep the trees dwarfed, much like those found near an alpine timber line. In Plate 2 is presented a glimpse of the edge of the stand in which No. 11 was growing. In Plate 3 there is given for comparison a view of a group of larger trees, growing under more favorable conditions and including No. 19. Dendrographic records of the wind-dwarfed tree (18 cm. in diameter at the height of the contacts) were begun in May 1924 and continued during the summer months for six seasons. Since the tree was not showing growth, the record was discontinued in 1929.

Ordinarily, little or no growth of redwoods is to be expected during the cold period of the year (MacDougal, 1929,² 28). However, in order to complete the record, the dendrograph was reattached in the summer of 1931, and continued in operation for 12 months.

An examination of the records reveals the surprising fact than in five out of the first six summers of study, the tree experienced a net decrease in diameter (table 5). During these same seasons another redwood, growing in a less exposed situation, and about 0.5 km. distant, increased steadily in diameter. The wind-dwarfed tree shrunk 3.7 mm., the control increased 27.0 mm.¹ From the 12-month record for the wind-dwarfed tree, begun in July 1931, it is seen that the tree experienced a net diametral shrinkage in this time, whereas the control tree showed an increase of about the same magnitude. Even during the moister and cooler half of the year (October 27 to April 22) the wind-dwarfed tree continued to shrink, while the control experienced little change.

While this wind-dwarfed tree was shrinking at the base, and possibly failing to form new wood on the lower bole, yet growth of the crown continued after a fashion. On a tree situated like this one, new shoots appear during the growing season, but many of them are killed within a few months. As a result, the crown consists of a very confused mass of irregularly branched stems and a complicated intermixture of living and dead leaves and twigs. The appearance of a representative branch from the crown of such a wind-dwarfed tree is shown in Plate 4. Although the tree studied dendrographically (No. 11) had not been really thrifty in recent years, yet it can not be considered that it was destined to die in the immediate future. The species is of such amazing vitality that it may be doubted whether the wind-action alone would have resulted in its death.

¹ For a detailed account of this tree's performance, the reader is referred to a recent paper of the writer (Haasis, 1933²).

TABLE 5—*Diametral changes,¹ in millimeters, of four redwood trees growing in Rocky Creek canyon (Monterey County, California).*

Period of record	Wind-dwarfed tree (No. 11)	Favorably situated tree, north exposure (No. 6, control for No. 11)	Decapitated tree, south exposure (No. 9—decapitated July 10, 1924)	Normal tree, south exposure (No. 8, control for No. 9)
May 6-July 10, 1924.....	+0.6	+1.6
July 10-Oct. 20, 1924.....	+0.1	-0.1
May 19-Oct. 18, 1924.....	-1.6	+3.8
May 22-Oct. 12, 1925.....	+0.4	+4.4	-0.2	+5.3
Apr. 15-Nov. 1, 1926.....	-0.2	+4.9	-1.2	+7.7
Apr. 19-Oct. 10, 1927.....	-0.1	+6.6	-0.6	+9.2
June 8-Oct. 29, 1928.....	-0.5	+1.8	-1.4	+1.9
June 2-Nov. 18, 1929.....	-1.7	+5.5	-0.2	+2.8
Apr. 22-Oct. 27, 1930.....	-0.3	+2.5
Oct. 27, 1930-Apr. 22, 1931.....	-0.5	+3.8
Apr. 22-Oct. 27, 1931.....	-0.5	+0.2
July 13-Oct. 27, 1931.....	-1.0	-0.1
Oct. 27, 1931-Apr. 22, 1932.....	-0.8	+0.1	-0.5	+3.7
Apr. 22-July 11, 1932.....	+0.1	+1.6
July 13, 1931-July 11, 1932.....	-1.7	+1.6	-0.4	+8.1
Apr. 22-Nov. 7, 1932.....	-0.3	+4.9
July 10, 1924-Nov. 7, 1932 (Total)	-5.6	+41.9

¹ Increase and decrease in diameter are respectively indicated by plus and minus signs.

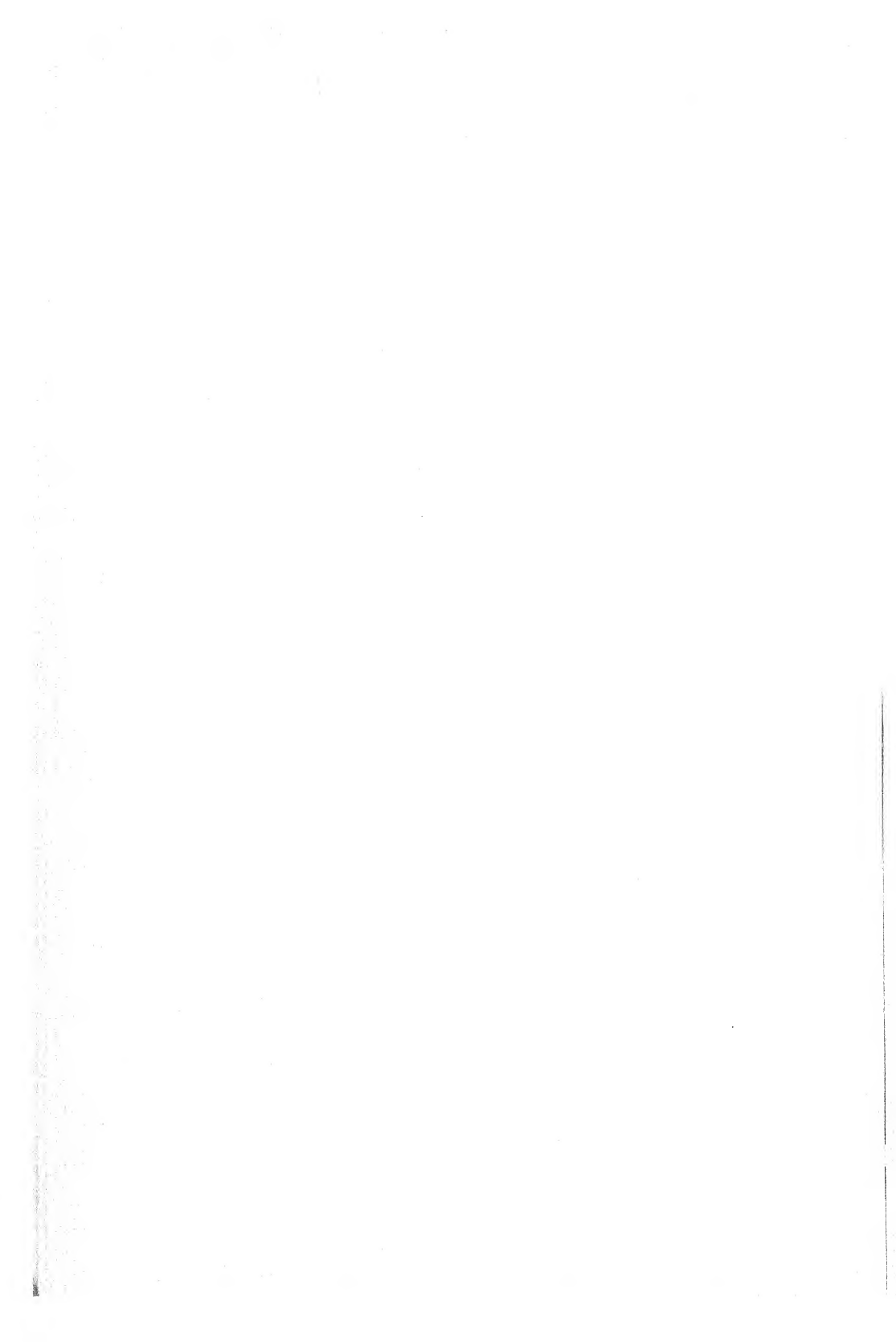
It seems quite likely, rather, that as adjacent shrubby redwoods and other trees slowly grew up to windward, they would have formed a protecting screen for this individual, allowing it to increase its height gradually, although probably always with a poorly developed top. Presumably a mass of even dead branchlets would have appreciable value as a windbreak. This tree appears to have been a sprout from the base of a bole killed to the ground by a severe fire in the year 1880 or thereabouts.

The other redwood (No. 9), in which shrinkage for a number of seasons was noted, stood on a somewhat dry southerly exposure, but was free from the excessive wind-movement to which the wind-dwarfed tree (No. 11) was subjected. It was located about 0.5 km. east of No. 11. This tree was cut off at a height of 2 meters in July 1924. Following decapitation it, too, shrunk quite consistently for several succeeding summer seasons. As a control for this experiment there is available another redwood (No. 8) 1 meter distant and of very nearly the same size. Records of diametral changes for these two trees are presented in table 5, while figure 15 gives a comparison of the changes during a 15-month period.

In the fall of 1932, more than 8 years after the traumatism, the decapitated tree was still alive. It was cut down in November and a detailed study made of the stem and branches. This examination showed that branches had begun to grow at or near the top in 1925, two of them attain-



Branch from wind-dwarfed redwood, cut at Rocky Creek in January; showing irregular branching and complicated intermixture of living and dead twigs, characteristic of this species growing on edge of stand and subject to desiccating winds. On some twigs of this branch all leaves are dead and gray, but short lateral shoots with new green leaves have appeared either on twig itself or at its base. Even on prominent green shoot at distal end of branch, the leaves of some laterals have turned brown in whole or in part. Green leaves themselves are much more yellow in color than on a normal branch. Scale



ing lengths of 2 and 3 meters, respectively, by 1932. These branches can not by any means be considered to have provided a food-producing plant equivalent to the cut top, which had been 5 meters long. Adjacent to the bases of these and other branches, patches of new growth of varying thickness were formed external to the layer of 1924 and becoming progressively thinner with increased distance from the branch. The greater part of the bole, however, shows no growth subsequent to that laid down in 1924. Nevertheless traumatism caused by cutting a small chip out of the tree, at a height of 7 dm. in September 1931, resulted in the stimulation of the dormant cambial tissues to the production the following year of a patch of new growth surrounding the wound. This 1932 layer is very similar in general appearance and relative location to the layers associated with leafy branches.

In September 1931, four living stems adjacent to the base of the decapitated tree, and apparently from the same root, were cut off close to the ground. The purpose of this treatment was to ascertain whether it would have any effect on the activity of the cambium of the trunk. No general resumption of growth on the bole could be detected as a result of this treatment. The dendrograph recorded continued shrinkage of the tree. Watersprouts, however, developed in considerable number during the season of 1932, and it is possible that if the tree had been left a few years longer the survivors of these small branches would have aided materially in covering the 1924 layer with new growth.

It does not seem to have been true during the years 1924-1931 either that the adjacent trunks contributed appreciably to the food supply of the decapitated tree or that they caused any notable drain upon the food supplies elaborated by its newly developing branches. It appears that these food substances had no opportunity to get far away from the bases of their parent branches before being deposited as new wood and bark.

From the above considerations it is evident that ring counts made near the base of a redwood tree may give an entirely erroneous index of its age if the tree has, at any time during its life, suffered a serious loss of crown.

TABLE 6—*Prolonged shrinkage of a palo verde, Pima County, Arizona.*¹

Date	Relative diameter	Change during half-year interval
	mm.	mm.
Feb. 25, 1929.....	0.0	..
Aug. 26.....	-2.5	-2.5
Feb. 24, 1930.....	-2.7	-0.2
Aug. 25.....	-3.0	-0.3
Feb. 19, 1931.....	-3.3	-0.3
Aug. 31.....	-3.7	-0.4
Feb. 29, 1932.....	-3.6	+0.1
Aug. 29.....	-3.2	+0.4
Feb. 27, 1933.....	-3.1	+0.1
May 29.....	-4.2	..

¹ The minus sign indicates a relative diameter less than that on February 25, 1929.

An additional example of long-period shrinkage comes from southern Arizona. A dendrograph was attached in the spring of 1929 to a 10-cm. tree of the leguminous species palo verde growing in Pima County near the Desert Laboratory of the Carnegie Institution. The contacts were seated on the intact bark. In the following four and a quarter years this tree showed more diametral shrinkage than increment, and at the end of the period had experienced a net change of -4.2 mm. The course of this shrinkage, by 6-month intervals, is shown in table 6, where the diameter of the tree at the beginning of the study is given as zero to simplify presentation of the figures. It is a notable fact, which is not shown by table 6, that as late as July 1932 the relative diameter was down to -3.8 mm., while on August 22 it was -3.1 mm.; that is, an increase of 0.7 mm. occurred within a 7-week period ending in late August. Equivalent increase in diameter did not take place in the preceding three summers.

It is evident that this tree has been subjected for the past few years to a period of extremely unfavorable conditions such as are not uncommon to plants of the desert. There is no reason for assuming that similar unfavorable conditions have not been operative, for greater or lesser periods of time during the years in which the tree has been attaining its present diameter of 10 cm. The growth of such a desert species must obviously be pictured as of a markedly halting type, with alternating periods of increase and shrinkage.

The prolonged shrinkage of both the wind-dwarfed redwood and the palo verde is evidently related to seasonal shrinkage. This long-period shrinkage is obviously dependent upon the continuance or prevalence for many months of such environmental conditions, unfavorable for growth, as result in seasonal shrinkage. While the plant can not survive indefinitely in an unfavorable environment of this sort, yet generally speaking those plants which are apt to be subjected often to it are likely to be very tenacious of life when the environmental factors become so unfavorable.

SHRINKAGE FOLLOWING INSTALLATION OF DENDROGRAPH

Before leaving this section, mention should be made of another cause of slight diminution in diameter. When the bark is pared down to prepare seatings for the contact rods, it sometimes happens that the dendrogram for the subsequent week shows a certain amount of shrinkage (*cp.* fig. 21). This does not invariably occur, however. It is obviously to be attributed to drying-out of the exposed tissues. Since living tissues are not interfered with, this shrinkage is hardly to be included with that following traumatism.

DIAMETRAL INCREASES

Increase in diameter of a plant stem may be the result of two different processes, namely, (1) actual growth including cell enlargement and maturation as well as cell division, and (2) rehydration or refilling with water of partially dried tissues. While true growth is of course the more important of the two, yet from the preceding disquisition on shrinkages of various kinds, it will be evident that rehydration must at times play a quite significant part as a cause of diametral increases. Although growth is fre-

quently looked upon as involving only irreversible changes in size, yet it would seem convenient to include in the concept of tree growth some cell enlargement which subsequently is temporarily lost as a result of desiccating influences.

REHYDRATION

Rehydration implies a previous shrinkage. Diurnal shrinkage in trees is regularly followed by a compensating nocturnal swelling, evidently due to rehydration subsequent upon a reduction in the evaporating power of the air. When temperatures are suitable and soil moisture adequate, growth (cell division and enlargement) may also take place during the night. The ensuing diametral increase would then be a combined resultant of the two causes, rehydration and growth.

Similarly, when rain or irrigation follows a period of dry weather during which seasonal shrinkage has occurred, the partially desiccated tissues apparently become rehydrated and swelling follows. Not infrequently this seems to be the chief if not the sole cause of the autumnal or hiemal swelling of pine trees in Monterey County, to which MacDougal has made reference (1924,¹ 10). At other times the water deficit appears to be soon satisfied and, if temperatures be favorable, true growth may begin

TABLE 7—*Course of shrinkage and enlargement at a height of 1 meter above the ground in Monterey pine No. 1 during 11 months of the years 1931 and 1932.¹*

Week ending	Net relative diameter	Week ending	Net relative diameter
1931	mm.	1931	mm.
Mar. 30	—0.14	Oct. 5	—1.60
Apr. 6	—0.09	12	—1.65
13	—0.32	19	—1.56
20	—0.41	26	—1.56
27	—0.23	Nov. 2	—1.70
May 4	—0.14	9	—1.70
11	—0.41	16	—1.15
18	—0.50	23	—0.79
25	—0.50	30	—0.70
Jun. 1	—0.09	Dec. 7	—0.75
8	—0.14	14	—0.61
15	—0.28	21	—0.61
22	—0.37	28	—0.38
29	—0.64		
Jul. 6	—0.41	1932	
13	—0.68	Jan. 4	—0.74
20	—0.68	11	—0.79
27	—0.82	18	—0.61
Aug. 3	—0.73	25	—0.61
10	—0.87	Feb. 1	—0.20
17	—0.87	8	—0.06
24	—0.96	15	—0.20
31	—0.96	22	—0.11
Sept. 7	—1.01	29	+0.34
14	—1.24		
21	—1.33		
28	—1.51		

¹The minus sign indicates a net maximal diameter less than that on March 23, the plus sign a greater net diameter.

almost immediately. This growth, commencing in November or December (cp. fig. 21) is simply the beginning of the annual growth increment which will occur chiefly in the following calendar year. A few examples will serve to make these relationships more vivid.

In the year 1931, one of the Monterey pines under observation (No. 1) increased in diameter through most of January, February and March (fig. 9). After this period, however, seasonal shrinkage began and continued with slight interruption until mid-November. Although increases were general in the weeks following, it was not until the end of February

TABLE 8—*Course of shrinkage and enlargement in redwood No. 6 during 8½ months of the years 1931 and 1932.¹*

Week ending	Net relative diameter	Week ending	Net relative diameter
1931	mm.	1932	mm.
Sept. 7	−0.14	Jan. 4	−1.09
14	−0.23	11	−1.27
21	−0.41	18	−1.22
28	−0.41	25	−1.40
Oct. 5	−0.55	Feb. 1	−1.26
12	−0.64	8	−1.26
19	−0.64	15	−1.49
26	−0.73	22	−1.49
Nov. 2	−0.82	29	−1.54
9	−1.05	Mar. 7	−1.54
16	−0.87	14	−1.40
23	−1.10	21	−1.31
30	−1.05	28	−1.17
Dec. 7	−1.23	Apr. 4	−0.99
14	−1.14	11	−0.81
21	−1.14	18	−0.73
28	−1.00	25	−0.69
		May 2	−0.44
		9	−0.19
		16	+0.06

¹The minus sign indicates a net maximal diameter less than that on August 31, the plus sign a greater net diameter.

that the total hiemal swelling had canceled the seasonal shrinkage which took place during the summer and autumn. In table 7 are presented figures to show the course of shrinkage and enlargement in this tree during the period under consideration. These are in the form of net diametral change, starting with the maximal diameter on March 23 as zero. The dendrograph (No. 1-A) with which these records were obtained was attached with its contacts about 1 meter above the ground.

In the case of a redwood (No. 6) very similar conditions prevailed, as is shown in table 8 and figure 9. This tree, 48 cm. in diameter, began to enlarge in March 1931 and continued its growth well into August. About the first of September shrinkage began, which was not completely compensated until the following May.

From tables 7 and 8, it will be seen that during the autumn each of these trees had shrunk to a diameter a millimeter and a half less than that which it had had a few months previously.

Winter phloem contraction reported by Brown (1915, 237), for northern white pine in New York, was followed in the spring by diametral increases which he referred to as "growth without cell division." In explanation of this, he suggested: "The awakening of growth is due apparently to the rise of soil water, with an accompanying increase in temperature." It now seems possible, that at least part of this increase may have been rehydration dependent upon a previously existing state of partial desiccation. Such drying may have been the cause of the hiemal shrinkage.

Another observation of diametral increase distinct from the results of cell division and enlargement is reported for western yellow pine by Pearson (1924) who writes: "A pronounced and sustained swelling, apart from actual growth, is recorded during long periods of rainy weather and a corresponding shrinkage in dry weather." Lodewick (1925), also, writes as follows of a similar occurrence, in the case of white ash, which came under his observation: "An appreciable precipitation is followed shortly by an increase in diameter, which is lost following the rainy period. This is not to be considered as growth, since no permanent increase in size results." Both Pearson and Lodewick based their statements on dendrographic records. As will be brought out later, true growth may have occurred during the period of rehydration. If so, we can simply consider here that complete rehydration of the dry tissues was effected at even later dates than would be indicated by tables 7 and 8.

Another case of bole swelling in November has been recorded by Romell (1925, 113, 123) for pine in northern Sweden. No adequate explanation is offered for this.

Excellent examples of the rehydrating effects of irrigation are afforded by the dendrographic records for coast live oak. In one irrigation experiment described by MacDougal (1921,¹ 33-34), the application of water to the roots of an oak tree (No. 2) of this species was begun in the evening, in August. Within two hours after the start of the irrigation a diametral increase occurred. This tree had begun to shrink in the week preceding irrigation, the amount for the week being 0.07 mm.

In July 1933, another coast live oak tree (No. 3) was supplied with water for 33 hours, beginning at 10 a.m. on the 26th. The subject of this irrigation was one of two boles from the same root system, the other bole (No. 2) having been the subject of the earlier experiment. Oak No. 3 carried three dendrographs, one (No. 3) with contacts on the outside of the bark (which was 8 cm. in diametral thickness), one (3-B) with contacts on the outermost wood at the bottom of conical holes cut in the bark, and the third (3-A) with contacts on wood perhaps 5 or 6 years old (at the base of holes penetrating the wood 2 or 3 cm. on each side).

The tree's maximal diameter for the first half of the year (on the basis of weekly summaries, as recorded by dendrograph No. 3) had been attained on May 8. During the 10 weeks subsequent to this day, the tree experienced a net shrinkage of 0.5 mm. In the week preceding irrigation, shrinkages were recorded by all three instruments. The soil moisture content on the 25th was about 5 per cent (based on the dry weight) at depths of 30 and 50 cm.

As a control for the irrigation experiment, another dendrograph was attached to a coast live oak (No. 4) of approximately the same size as No. 3 and standing 3 dkm. distant. The contact rods were seated on the intact bark (which had a diametral thickness of 11 cm.). This tree also experienced shrinkage in the week preceding irrigation of No. 3.

The effects of irrigation were evident within a few hours (fig. 18). During the 24-hour period following irrigation a marked increase in diameter

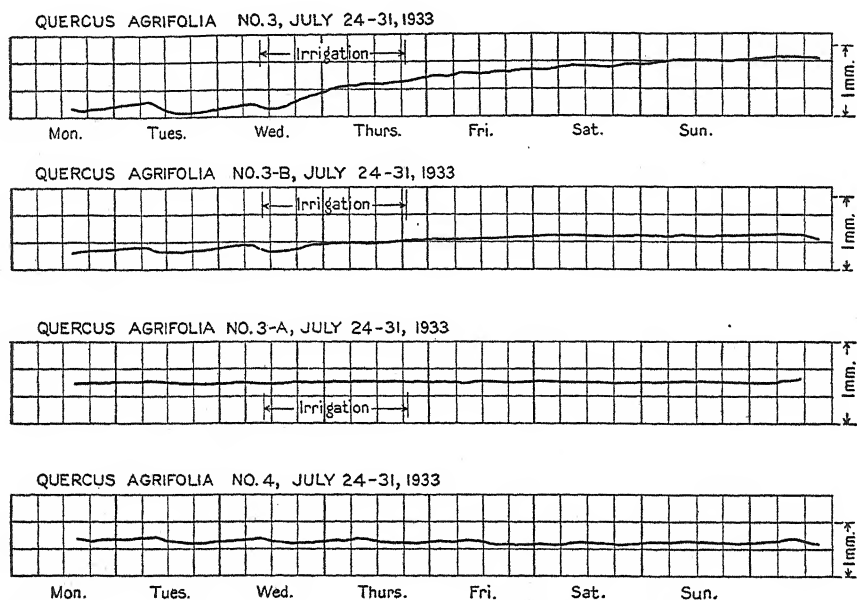


FIG. 18—Effect of irrigation on coast live oak. Instruments Nos. 3, 3-B and 3-A were attached to experimental tree; No. 3 with contacts on intact bark, 3-B with contacts on wood from which bark had been removed, and 3-A with contacts at bases of holes penetrating wood 2 or 3 cm. No. 4 was control tree situated near experimental tree but at such distance as to be uninfluenced by irrigation. Dendrographic contact rods were seated on intact bark of control. Note reduction or obliteration of diurnal fluctuation on days following irrigation. Seasonal shrinkage in entire tree (No. 3) for ten weeks preceding irrigation was canceled in four days. The woody cylinder (No. 3-B) had been increasing in diameter for several weeks prior to irrigation, but in week immediately preceding it had experienced shrinkage. Diametral increases for two or three weeks after irrigation were appreciably greater than they had been for month preceding.

occurred in the entire tree, and increases of lesser magnitude in the woody cylinders. The control did not show a net change.

Diurnal shrinkage was not shown by instrument No. 3 on the 27th and 28th, although a slackening of the rate of increase occurred during the middle of the day. On the 29th and 30th, the diurnal shrinkage was scarcely discernible at the magnification used. No. 4, however, showed regular diurnal shrinkages on the 27th and succeeding days. The net

diametral changes for the 5-day period from 8 a.m. July 26th to 8 a.m. July 31st and for the ensuing week were as follows:

	July 26-31 (8 a.m.-8 a.m.)	July 31-Aug. 7 (8 a.m.-8 a.m.)
Entire tree (S).....	+0.63 mm.	+0.14 mm.
Woody cylinder (S-B).....	+0.12	+0.23
Inner woody cylinder (S-A).....	0	+0.06
Control (4).....	-0.05	-0.15

The seasonal shrinkage of the 10 weeks preceding irrigation was canceled in 4 days. Diametral increase continued in the entire tree until August 10. At this time the records showed a total for the two weeks since the beginning of the irrigation of 0.85 mm. Enlargement of the woody cylinder continued until August 24. The total increase experienced for the four weeks following irrigation was essentially the same as for the entire tree in the shorter period, namely 0.80 mm. No rain fell during the month following irrigation, although some of the days were overcast.

MacDougal has described an instance of rehydration after shrinking which followed girdling without exposure of the inner tissues to desiccation (1924,¹ 17-19; 1925,¹ 64). In this case water was supplied through the ends of cut branches. In two weeks there was a cancellation of one-fourth of the contraction which the tree had experienced during the preceding 5 weeks. The experimental subject was a Monterey pine (No. 21).

GROWTH

CONTROLLING FACTORS

The chief conditions necessary for arboreal growth and subject to considerable variation are an adequate moisture supply and sufficient heat. The adequacy of the moisture supply is governed by a number of diverse factors, among which may be mentioned the character of the soil and the relative time of precipitation. Where rain is plentiful during the warmer period of the year, there trees are likely to flourish. In some instances, precipitation preceding the warm period holds over and meets the trees' needs. A number of observers have reported on studies of such relations (Kirkwood, 1914; Pearson, 1918, 1924; Robbins, 1921), but the details of these need not concern us at present.

As has been mentioned, in Monterey County we have to deal with a climate which is characterized by a deficiency of rain during the warmer part of the year. Except in occasional small patches, the soil moisture in the area occupied by Monterey pine is rapidly reduced to a very small amount. The broad result in the case of Monterey pine is, accordingly, that growth must take place largely during the rainy season, if it is to occur at all. With redwood, on its native sites (marked by a better supply of underground water), the situation is less critical, although the grosser climatic features are the same as for Monterey pine.

An effort has been made to ascertain approximately the temperatures favorable for growth by the use of small thermometers, a decimeter or two long, inserted diagonally into the bark of experimental trees. These thermometers are so set that the bulb lies in the general region of the cambium, with bark on one side and wood on the other, the junction of bark and thermometer stem being sealed with the modeling clay sold as Plasteline. The installation is commonly on the north side of the tree about 1.5 meters from the ground.

At one time or another cambial thermometers were maintained in Monterey pine, coast live oak and Arizona walnut at Carmel, and redwood, bigleaf maple and California laurel at Rocky Creek.

These observations do not indicate the existence of any marked correlation between the cambial temperatures in the trees studied and the air temperatures recorded by a thermograph at Carmel. Neither is there a correlation between cambial temperatures and those recorded by a thermometer hung to the outside of a pine tree a few centimeters from the cambial thermometer.

The only generalizations which it seems possible to make are a reiteration of previously published statements (Haasis, 1931⁴): "In general the temperature of the cambium follows that of the air, but does not reach the same extremes. . . . There is an indication that when the air temperature begins to change after reaching a day's extreme, the cambium temperature may sometimes begin to change similarly before the two become identical. . . . Further study is needed to establish or disprove this apparent phenomenon." These conclusions were based primarily on comparisons made with a small thermometer hung outside of the tree (Monterey pine No. 17) near the stem of the cambial thermometer. A comparison of the Carmel thermograph temperatures with those of the thermometer in the cambium of Monterey pine No. 1 adds some support to the truth of the apparent phenomenon mentioned. It is not clear, however, why the tree temperature, already lower (or higher) than that of the air, should fall (or rise) in this way. It is to be remembered, too, that there may have been slight temporary differences between the temperature conditions in the thermograph shelter and those at the base of Monterey pine No. 1, the two being situated 12 dkm. apart horizontally and 5 meters vertically. A comparison of air temperatures in the thermograph shelter and on the north side of Monterey pine No. 17 on a few days shows that while there is a general accordance between the two, there may be a difference of as much as 3° C. These two thermometers were 7 dkm. apart horizontally and 16 meters vertically, one being located on the dune, the other in the lower garden.

Two graphs published by Harvey (1923, figs. 3, 4) indicate for an apple tree a similar relation between cambial and air temperatures as is suggested for Monterey pines, the cambial temperature being shown as changing before the temperature of the air reached that of the cambium. When the air temperature began to fall, in some cases the cambial temperature fell also before the two coincided. In other cases, with rising air tem-

perature, the cambial temperature rose before the two became the same. Harvey used thermocouples for both air and cambial readings.

On the basis of such cambial temperature readings, MacDougal (1930⁴) has reported the observation that when the temperature of the cambium falls to 8° C. for even a few hours in the morning, no increases in diameter can be expected for that day in Monterey pine trees. Even though the temperature rose as high as 16° during the afternoon, diametral increase did not ensue.

The records for redwood and California laurel, although admittedly lacking in completeness, suggest that for these species, too, the critical temperature is in the neighborhood of 8° C. The favorable temperature for leaf opening or diametral growth in the deciduous bigleaf maple is not clear from the available records.

While, in general, a nocturnal cambial temperature of 8° C. or above appears to be necessary for growth in the three evergreen species men-

TABLE 9—*Diametral increase in Monterey pine No. 33 in spite of low nocturnal temperatures.*

Date 1932	Cambial temperature, 8 a.m.	Highest observed cambial temperature for day, at various hours	Increase in diameter, 24-hr. period ending on indicated date
	°C.	°C.	mm.
Feb. 15	1.5	13.5	..
16	4.0	12.0	0.1
17	1.5	14.0	0.1
18	2.5	13.5	0.1
19	2.0	12.5	0.1
20	4.0	8.0	0.1

tioned, apparent exceptions to this have been observed. In a few cases diametral increases have occurred in Monterey pine, even when the nightly minimal temperatures were well under 8°. Such conditions have been observed at one time or another for three trees at Carmel, one near the top of the dune and the others in the lower garden. The most interesting of these records is afforded by one of the latter (No. 33) in which there was steady diametral increase for a period of five days in February 1932 although the cambial temperatures dropped to 4° or below each night. The cambial temperatures at 8 a.m. during this half decade are listed in table 9, together with the maximal cambial temperatures observed at various hours and the diametral increment, day by day. This tree had been growing steadily for some time past (fig. 14).

It seems entirely probable that under usual conditions the relation of growth to temperature can be summed up as follows: Cell division can not take place except when the cells are turgid or nearly so. The growing tissue is ordinarily not turgid at those times when the dendrograph records diametral shrinking. Growth, therefore, is not to be expected during the

daytime in clear weather. Furthermore, cell division can not take place when the temperature of the cambium is below a certain grade, which may tentatively be regarded as 8° C., for Monterey pine. If, therefore, the temperature is below this critical point during the period when the water in the cells is sufficient for cell division, growth will not take place in spite of the complement of green leaves. These conditions would obtain on cool nights. Conversely, if the water in the cells is inadequate for cell division, which at least in times of drouth appears to be the common condition during daylight hours and perhaps at night also, then, too, cell division can not take place even though the temperatures are sufficiently high.

If the foregoing is the explanation of the general situation, then some additional factor must be looked for in the less usual cases where higher temperatures during the warmer part of the day can stimulate growth in the evergreen plant. The indications are that when moisture conditions are especially favorable, cell division may take place in the cambium, during the daytime, despite the fact that the tree as a whole suffers a diametral decrease. Such a possibility will be taken up again a little further on.

There are also to be considered a few other factors which might produce the observed effect. Rain of course would be followed by diametral increase if the plant tissues were comparatively dry. That this was the case with Monterey pine No. 33 in mid-February, however, seems unlikely. It had not suffered seasonal shrinkage in the months preceding (fig. 14). Rain, too, is less likely to fall on the cooler days. The only precipitation for the days indicated in table 9 was 4 mm. for the 24-hour period ending at 8 a.m. on the 16th.

Observations by various workers have been taken to indicate that light has an inhibiting effect upon plant growth.¹ This effect has been reported for aquatic as well as for terrestrial forms. Nevertheless, from the above consideration it seems highly probable that in some cases or in part it is to be attributed rather to other factors than the light *per se*. Periods of daylight are commonly concurrent with periods of relatively low humidity and relatively high temperature. Inasmuch as these latter are conditions which favor evaporation and so a greater or less degree of cell flaccidity, this fact of itself appears sufficient to account for a considerable part of the reduction of growth rate or lack of growth which has been observed during the daytime, a possibility suggested by MacDougal (1903, 308) many years ago, and substantiated by some studies of Lloyd (1916).

That light of itself need not necessarily be unfavorable for growth is demonstrated by experiments of Harvey (1922¹) in which 24-hour illumination was used with such satisfactory results that the author ventures the opinion that "it ought to be possible . . . to grow three generations . . . within one year." It has even been suggested by MacDougal (1903, 308) that "the actual constructive processes . . . may continue uninterrupted during the apparent decrease or cessation of growth" occasioned by loss of water through accelerated transpiration in daylight. Lodewick (1925, 318-319) states on the basis of some of his observations that there is a sugges-

¹ See, for example: Jost (1907, 302 ff.), Palladin (1926, 277), Pfeffer (1903, 98).

tion that cell division took place at a time when the tissues of a tree were not fully distended.

Some of the dendrographic evidence indicates that, when water is plentiful and temperatures high enough, growth may take place without interruption by diurnal shrinkage. One example is afforded by growth records procured with a modified dendrograph set about a plant of maize (No. 1). This was a small plant about 5 or 6 weeks old growing under glass. The bearing points of the instrument were on leaf bases above the third leaf, 11 cm. above the soil surface and about 5 cm. above the top of the stem. The diameter of the stem between contact points was 1 cm.

On some days this plant showed only very slight diurnal shrinkage, occasionally amounting merely to a reduced rate of growth. A copy of a dendrogram illustrating this is given in figure 3. This plant had been irrigated on the 21st of March, and irrigation took place again on the 28th. With this graph may be compared that for the same week of a Monterey pine tree (No. 20) growing outside and 1 dkm. distant, also shown in figure 3. The weather during this week was partly clear, partly overcast, and occasional light showers occurred. March 23, the 25th and the 26th were prevailing clear, as well as the afternoon of the 24th. In the case of trees of the usual type, such reduction of diurnal shrinkage as that exhibited by the maize plant has been shown by the dendrographic records to occur during wet weather (fig. 2) or after irrigation (fig. 18). The giant cactus sometimes affords examples of sustained enlargement without diurnal shrinkage, similar to that of the maize plant, as shown in figure 19. There was no precipitation on the first six days of the period covered by this record.

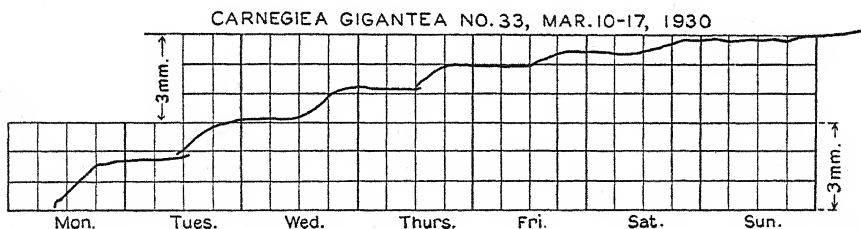


FIG. 19—Dendrogram illustrating sustained enlargement in giant cactus, without diurnal shrinkage, or with very slight diurnal shrinkage, in absence of rain; Tucson, Arizona. Precipitation during period indicated consisted of 13 mm. (0.52 in.) on 16th and 26 mm. (1.02 in.) on 17th, no rain falling in earlier part of week. Breaks in graph are due to disturbances of instrument.

It is entirely possible that during any given week, cell division and enlargement may take place even though the net diametral change for that week is negative. We can picture a situation somewhat as follows: Early in the week a period of warm, rainy weather would be favorable for the multiplication and enlargement of cells. Dry, clear weather following this would permit loss of water both from the older tissues and from the newly formed cells. The net result could then easily be a shrinkage for the week. It is unlikely, however, that cell division can occur when the mother cells are not turgid.¹

¹ See Palladin (1926, 244), Pfeffer (1903, 118).

Such a state of affairs as has just been suggested is illustrated by figure 20, a copy of a dendrogram for Monterey pine No. 20. This tree had not experienced seasonal shrinkage during the summer and fall of 1925, although there was no growth for the week ending November 9 and a shrinkage of 0.1 mm. for the week ending the 23d. The diametral increase of 0.5 mm. the following week was more than enough to cancel this shrinkage. Rain totaling about half an inch (15 mm.) fell early in the week beginning November 30, with temperatures of 10° to 15° C. (50° to 60° F.). The diameter of pine No. 20 increased in response to the rain and mild weather for a couple of days. The latter part of the week, however, was rainless and the temperature rose above 21° C. (70° F.) on three successive days. During this period the tree shrunk to a notable extent, and the diameter at the end of the week was 0.3 mm. less than at the beginning.

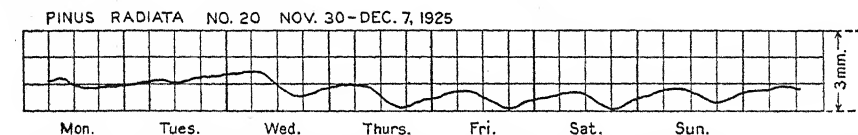


FIG. 20—Dendrogram for Monterey pine tree, illustrating growth incident to rain and mild weather in early part of week, but with a net shrinkage for week.

It would seem obvious that when temperature and moisture conditions are favorable throughout the year, trees would exhibit continuous growth (except perhaps for diurnal fluctuations). That such is the case in some tropical regions is commonly accepted as a fact. On the basis of dendrographic studies, MacDougal has reported instances of essentially continuous growth for a native Monterey pine at Carmel (1924,¹ 7-8, 11-12; 1929,² 30; 1930,⁴ 340, 342-343). Besides the tree (No. 17) which forms the basis of MacDougal's reports on this phenomenon, at least two other pine trees (Nos. 20 and 33) and a Monterey cypress (No. 2) have also exhibited essentially continuous growth in some years.

The fact of uninterrupted growth is based upon fortnightly summations of diametral change, as shown in table 10. It will of course be evident from the consideration in the earlier part of this paper of shrinkages of various kinds, that increase in diameter can not be regarded as strictly continuous if diametral decreases of any kind take place. If the records for the above-mentioned trees were summed by weeks instead of by fortnights, the periods of continuous growth would be shorter than shown. If, moreover, computations had been based on other fortnightly periods, a net decrease would sometimes have been shown instead of a net increase. In the case of Monterey cypress, for example, weekly changes in 1931-32 were as follows:

Week ending		Change
Dec.	21	+0.05 mm.
	28	+0.18
Jan.	4	-0.32
	11	+0.36

The changes for the fortnights ending December 28 and January 11 were accordingly both *increases*, as shown in table 10. If, however, computations had been made on the basis of other groupings of the weeks, the change for the fortnight ending January 4 would have been a *shrinkage* of 0.14 mm. Going a step further, if the diurnal shrinkages (figs. 23, 26) are taken into consideration, there would be few periods of continuous swelling as much as a week in length.

TABLE 10—Fortnightly diametral increases in millimeters illustrating continuous growth in coniferous trees, Monterey County, California.

Fort-night ending	<i>Pinus radiata</i> No. 17	<i>Pinus radiata</i> No. 20	Fort-night ending	<i>Pinus radiata</i> No. 33	Fort-night ending	<i>Cupressus macrocarpa</i> No. 2
1925			1931		1931	
Jan. 5	1.10	0.30	Jan. 12	0.36	Oct. 19	0.45
19	1.05	0.35	26	0.45	Nov. 2	0.40
Feb. 2	2.00	1.15	Feb. 9	1.59	16	0.20
16	1.10	1.50	23	0.77	30	0.10
Mar. 2	0.95	1.45	Mar. 9	0.77	Dec. 14	0.25
16	0.80	0.95	23	1.05	28	0.25
30	0.70	0.95	Apr. 6	0.86		
Apr. 13	0.85	0.75	20	1.14	1932	
27	1.15	1.15	May 4	1.23	Jan. 11	0.05
May 11	1.75	1.10	18	1.28	25	0.30
25	2.90	1.35	June 1	0.82	Feb. 8	0.65
June 8	2.20	2.00	15	1.05	22	0.40
22	2.85	0.85	29	0.18	Mar. 7	1.10
July 6	2.20	1.75	July 13	0.55	21	0.75
20	0.70	1.60	27	0.45	Apr. 4	1.50
Aug. 3	1.00	1.30	Aug. 10	0.77	18	1.15
17	2.15	1.45	24	0.27	May 2	1.10
31	2.30	1.25	Sept. 7	0.64	16	1.35
Sept. 14	2.60	0.80	21	0.14	30	1.30
28	1.55	0.90	Oct. 5	0.05	June 13	0.15
Oct. 12	1.65	0.65	19	0.32	27	0.50
26	1.60	0.70	Nov. 2	0.18	July 11	0.81
Nov. 9	1.15	0.30	16	0.64	25	0.90
23	0.95	0.15	30	0.27	Aug. 8	0.67
Dec. 7	1.00	0.20	Dec. 14	0.05	22	0.72
21	0.90	0.55	28	0.59	Sept. 5	0.27
					19	0.63
1926			1932		Oct. 3	0.91
Jan. 4	1.10	0.55	Jan. 11	0.45	17	0.23
18	1.45	0.20	25	0.73	31	0.19
Feb. 1	1.40	0.55	Feb. 8	1.23	Nov. 14	0.41
15	2.35	1.30	22	0.91	28	0.36
Mar. 1	1.40	1.20	Mar. 7	1.86	Dec. 12	0.36
15	1.75	1.45	21	1.18	26	0.37
29	2.20	1.25	Apr. 4	1.23		
Apr. 12	1.20 ¹	1.25	18	1.27	1933	
26	1.65	1.20	May 2	1.32	Jan. 9	0.68
May 10	2.20	1.10	16	1.86	23	0.45 ¹
24	2.45	1.30	30	1.50	Feb. 6	0.05
June 7	1.65	1.00	June 13	1.09	20	0.32
21	1.45	0.75	27	1.18	Mar. 6	0.91
July 5	2.05	0.70			20	0.59
					Apr. 3	0.59

¹ 1 week's record missing.

It is possible that some tropical species may actually be found to show continuous increase in diameter, without any decreases, for appreciable periods of time. This phenomenon would logically be looked for in an evergreen tree growing in a climate characterized by the absence of definite dry and definite cold periods. Examples of climates of this type are found in the Amazon basin and the Philippine Islands (Schimper, 1903, 285).

One of the most extensive studies of cambial activity and growth-ring formation in the tropics has been made by Coster (1927) who worked with increment-borer cores and cross-sections of stems. He states: "There are only comparatively few species of woody tropical plants in which the formation of growth rings is entirely absent under uniform external conditions, while with dissimilar external factors beautiful growth rings are formed" (38, 108). In another place he notes that as nearly as he could judge, the cambium of the exotic *Taxodium distichum* was always more or less active at Tjibodas in western Java (7° S. Lat.), although at any one time great variation was to be observed in the stage of ring formation on different parts of the tree (37, 132-133). Nevertheless growth rings of a normal type were formed (37, 132). Among the noteworthy results of Coster's study is the observation that individual plants of a large number of exotic trees which are deciduous in their native countries remained evergreen at Tjibodas. The climate here is characterized by a monthly rainfall of 100 to 400 mm. (4 to 16 in.), although in the season of June-October dry periods of several weeks' duration occur (37, 55-57). Besides the conifer *Taxodium distichum*, these exotic trees included the angiospermous species *Alnus maritima* Nutt., *Fagus sylvatica* L., *Castanea sativa* Mill., *Quercus pedunculata* Ehrh., *Pyrus malus* L. and *Acer palmatum* Thunb. (37, 131-156). Sometimes the green leaves are found to be confined to only a few branches.

Among the native species, Coster observed the greatest diversity in the leaf-periodicity and even in the same species growing in different climatic regions of the island (38, 2-8). In the relatively equable climate of western Java, leaf fall sometimes occurred a branch or two at a time, so that the tree was never wholly bare, whereas the same species in the drier eastern part of the island experienced a definite dry-weather leafless period. The program of these species was, accordingly, much like that of some of the species brought in from different parts of the world. In a few cases the leaf fall in the west took place every 8 months instead of annually, as in the east.

For a subtropical species, stinkwood, Phillips (1927²) has stated on the basis of dendrographic studies that growth is apparently not limited by seasons.

It is obvious that where the warm season may be prevailingly dry and the moist season prevailingly cold, evergreenness would be a distinct asset to a plant. Such a habit would enable it to take advantage of occasional periods, even of very short duration, when moisture conditions were favorable during the warm part of the year or when temperature conditions were

favorable during the wetter season (*cf.* Cooper, 1922). The exhibition of continuous growth must obviously be based upon an evergreen state.

PERIOD OF GROWTH

In the case of Monterey pine, as it is found in nature, growth, or at least increase in diameter, can be expected to cease during the normally dry weather of summer and fall. With the advent of rain in the fall or winter, growth will be resumed, provided the temperature is high enough; and as long as the amount of heat available is inadequate, growth will not begin. It may therefore be January, February or even March before the year's growth is well started in this species.

On the other hand, diametral increase may be stopped by soil desiccation in the summer time in spite of favorable temperatures for growth. If, then, such a dry period be interrupted by rain, growth can be expected. An example of such conditions is shown in the graphs for Monterey pine Nos. 1 and 28 in figure 9. In this instance shrinkage was checked and the direction of diametral change reversed when rain interrupted a comparatively dry period, in May 1931. Incidentally, if growth stops definitely enough during the dry period, two internodes and two growth rings may be formed for the year in which the dry weather is thus broken.

During the fall and winter of 1931, Dr. I. W. Bailey kindly made for the writer a series of microscopic examinations of wood from a couple of Monterey pine trees growing at Carmel. Of these trees, one was 7 cm. in diameter and stood near the top of the fixed sand dune on the grounds of the Coastal Laboratory. The other was growing near the base of the dune and measured 13 cm. in diameter. Dr. Bailey's reports on these samples are as given in table 11.

TABLE 11—*Autumnal condition of the wood in two Monterey pine trees.*

Date of cutting sample	Top of dune (dry)	Base of dune (moister)
Oct. 8, 1931	Tree still in process of differentiating the "latewood"; possibly some cell enlargement and even cell division.	"Latewood" in last stages of formation, <i>i.e.</i> outermost tracheids forming secondary walls; no evidence of cell division or cell enlargement; cambium apparently nearly in resting condition.
Nov. 7, 1931	Annual ring apparently completely differentiated; cambium probably in a resting condition; cambium has not passed into a stage entirely comparable to that which occurs in the conifers of the northeastern United States; nuclei have not taken on the elongated form common in these eastern species; cambium resembles root cambium of some eastern species.	Annual ring still in process of differentiation, <i>i.e.</i> 15-16 tracheids at end of ring have not completely differentiated; cambium must be at least slowly active.
Dec. 30, 1931	Summer wood ends abruptly and there is a fairly wide zone of young new tracheids that have enlarged but have not formed secondary walls as yet; in other words, there appears to have been considerable growth during December, so that a considerable portion of the new ring has already been formed.	

The tree near the top of the dune occupied a site comparable to those of Monterey pines Nos. 1 and 6. The site of the lower tree was somewhat like that of Nos. 17 and 33, but probably a trifle drier. The former stood about 1 dkm. from No. 6, the latter 2 dkm. from No. 17 and 4 dkm. from No. 33. These microscopic observations substantiate the dendrographic records of nearly continuous growth for trees whose water supply is adequate throughout the year. They also indicate that part of the hiemal swelling may be attributable to cell division and enlargement distinct from rehydration. It would seem that these diametral increases should very likely be regarded as a combination of the two processes. As will be seen by reference to figure 9, an appreciable amount of rain fell between November 7 and December 30. Bailey's observations show the completion of one growth layer and the beginning of another during this period. But it should be recalled on the other hand that at least one of these trees (at the top of the dune) even by the end of December probably had not regained the diametral losses which it had suffered during the dry summer months (see table 7).

Obviously there may be all sorts of intermediate programs of diametral change between those cases where growth is continuous throughout the year and those where a long period of shrinkage occurs in the summer or autumn. The year-by-year history of even an individual tree may exemplify these differences, as may be seen by reference to figure 21. In this series of graphs are shown the diametral changes recorded by two dendrographs on a Monterey pine tree (No. 1) for a period of 13 years. The contacts of the lower of these instruments were 1 meter above the ground, those of the upper 7 meters higher. The height of this tree was 26 meters in 1933. The diameter at 8 meters was 48 cm. in the same year, and at 1 meter from the ground 59 cm. In 1920 the diameters were 41 cm. and 32 cm., respectively (MacDougal, 1921, 23). The indicated seasonal period (approximately April-March) was chosen to include in each graph reattainment after seasonal shrinkage of the diameter which the tree had had at the beginning of this contraction.

As will be seen in figure 21, an instance of annual growth beginning in the autumn after a comparatively short period of shrinkage is afforded by the records (of the lower instrument) for 1927-28. In this case seasonal shrinkage did not start until toward the end of August. The total amount was relatively slight, and the beginning diameter was fully reattained before the middle of December. After this, steady growth continued until seasonal shrinkage again set in about the middle of the year 1928. It is evident from these figures that the 1928 growth of this tree began not later than the middle of December 1927.

In the winter of 1922-23 growth was essentially continuous at the lower instrument. In 1923 a shrinkage beginning in August was canceled in 4 weeks. After this, growth continued until another 4-week period of shrinkage and compensating enlargement in November and December. Presumably in this case also we can consider that the 1924 growth began in December of the preceding year.

Another Monterey pine tree (No. 6) started its new growth for 1927 yet earlier in the season. After the summer growing period of 1926, this tree first began to shrink in August. This shrinkage was not wholly uninterrupted and before the middle of November it had definitely ceased (table 12). The diametral loss was quickly made up and sustained increases ensued for several months. From these examples it is clear that even in the North Temperate Zone the annual growth of a tree under certain climatic conditions may begin well before the first of the calendar year. This is of course a corollary to the possibility of continuous growth already discussed. It also indicates that in some cases the observed autumnal increases in diameter may be due to the beginning of true growth rather than merely the result of rehydration of desiccated tissues.

TABLE 12—*Autumnal commencement of growing season, Monterey pine No. 6.*¹

Week ending	Net relative diameter	Week ending	Net relative diameter
1926	mm.	1926	mm.
Aug. 23	−0.1	Nov. 1	−0.1
30	0.0	8	−0.2
Sept. 6	+0.1	15	+0.2
13	+0.2	22	+0.4
20	+0.1	29	+1.3
27	−0.1	Dec. 6	+1.7
Oct. 3	+0.6	13	+1.7
11	+0.4	20	+2.0
18	+0.4	27	+2.2
25	+0.2	1927	
		Jan. 3	+2.9

¹ The minus sign indicates a net maximal diameter less than that on August 16, the plus sign a greater net diameter.

An additional fact in support of the view just enunciated is afforded by the parallel records for two Monterey pine trees (Nos. 6 and 23) of which one had been defoliated. In August 1924 No. 23 had been growing faster than No. 6. Defoliation was performed upon No. 23 the end of August. In September the diametral *decrease* of No. 23 was greater than that of No. 6. In November and December No. 6 swelled appreciably (more than canceling the preceding shrinkage) while No. 23 definitely contracted. This suggests that the winter increase in diameter is at least in part due to the formation of new tissue dependent upon the presence of green leaves.

From the foregoing considerations, it is clear that it may sometimes be quite difficult to decide just when a tree's annual growth begins. In a country in the North Temperate Zone having a mild winter climate following a dry warmer period, the new growth of an evergreen tree for any given calendar year may start in the preceding December or November. If any appreciable shrinkage has occurred prior to this, rehydration may also occur at this time of year, either concurrently with the growth or just before it. If rehydration must take place before growth, it is obvious that the ascertaining from dendrograms of the time at which growth begins must

take into consideration the preceding seasonal shrinkage as well as the diametral increases.

Furthermore, if dendrographic or other detailed measurements be begun of a tree which has recently experienced shrinkage, any diametral increases observed will include those due to rehydration as well as those which are the result of growth. If, for example, shrinkage occurs during the winter, then measurements begun in early spring might easily give erroneously high values for the year's growth.

In the earlier dendrographic studies of redwood, the chief interest centered on the course of diametral enlargement. The instruments were accordingly operated from April, May or June to October or November, the average dates of beginning and ending being April 22 and October 27, giving a period of 6 months.

For the most part, the trees studied exhibited increases in diameter during these periods of operation. Some of the records, however, showed that exceptions to this general truth occurred, and in later work instruments were run through the winter to help establish with greater precision the period of diametral growth for the species.

The wind-dwarfed redwood and the decapitated redwood already discussed (in section on Traumatic and Prolonged Shrinkage) afford examples of trees which shrunk appreciably during the period of dendrographic study (table 5). In the one case environmental conditions were unfavorable; in the other, loss of the major part of the crown interfered with the plant's normal development.

In addition to these two, the dendrograms for another redwood tree show that in many years it, also, experienced definite seasonal shrinkage beginning in extreme cases as early as mid-June. This tree (No. 8) was 2 dm. in diameter and stood on a south-facing slope, near the upper edge of the stand and 1 meter from No. 9. For other redwoods (Nos. 6, 10 and 14) on the northerly slope of the opposite side of the canyon, such seasonal shrinkage was in general less marked. Without going into a detailed analysis of the records, it may be said that sometimes the shrinkages began later in the season than those of No. 8; sometimes they were of lesser magnitude; and sometimes they were entirely absent during the periods of study. It was only rarely that the shrinkage was less marked in No. 8 than in the trees on the opposite north-facing slope. Presumably the difference is attributable to the fact that usually the soil with the north exposure did not become as dry as that of the other side of the canyon. While few studies have been made of soil moisture conditions on these two slopes, the following figures are suggestive:

Location	Depth of sample	
	30 cm.	50 cm.
South exposure, near redwood No. 7_____	8 p. ct.	7 p. ct.
North exposure, near redwood No. 10_____	13	12

Each of these percentage figures is the average of the values for two samples (based on the dry weight of the soil). The samples were taken early in July of the notably dry summer of 1931. In some years the direction of the wind may have been responsible for the occasional anomalous

relations mentioned. The site of redwood No. 8 is evidently less favorable than that of Nos. 6, 10 and 14, although considerably more so than the windy location of No. 11. Another redwood tree (No. 7), however, 5 dm. in diameter and standing 2 meters distant from No. 8, also failed to experience such pronounced seasonal shrinkages in summer and autumn as those of No. 8. Perhaps this is to be ascribed to a better development of the root system than that of its companion, which made it less susceptible to drying out of the soil. These trees stood 14 meters above Rocky Creek, and it is quite possible that some of the roots of No. 7 extended down as far as the stream level, while those of the smaller tree (No. 8) had not yet attained sufficient length for this.

From the above it appears that the growing season of individual redwood trees may be terminated by shortage of soil moisture long before the end of October. Aestival and autumnal seasonal shrinkage may occur for several months before that time. With the extension of the records through the winter period, October-April, it became evident that in addition to the aestival-autumnal decreases, hiemal shrinkage also is to be expected. This has been observed for Nos. 6, 7, 8 and 10 (on both north and south slopes) and for a large tree, 14 dm. in diameter (No. 19). The last-mentioned tree was growing in a tongue of the Rocky Creek stand extending northward up a small dry hollow and including several other large trees (Plate 3). There is even a suggestion of the beginning of such diametral decreases (in October for three years) in the case of a 2-dm. tree (No. 13) growing on a notably moist site. Winter records of this tree were not obtained, and it is therefore impossible to ascertain the extent to which this shrinkage was prolonged.

At the other end of the summer season, too, diametral increase may take place before the middle of April (*Sequoia sempervirens* No. 8, fig. 9); and, on the other hand, hiemal shrinkage may be still uncompensated by the middle of April. This is exemplified by the performance of the 55-cm. redwood No. 7 during the winter of 1932-33, as shown in table 13.

TABLE 13—Shrinkage and enlargement of redwood No. 7, winter of 1932-33 and spring of 1933.

Date	Relative diameter	Date	Relative diameter
1932	mm.	1933	mm.
Nov. 14	0.0	Feb. 6	-0.81
21	-0.05	13	-0.76
28	-0.32	20	-0.99
Dec. 5	-0.41	27	-1.04
12	-0.36	Mar. 6	-1.04
19	-0.27	13	-1.04
26	-0.54	20	-0.99
1933		27	-0.94
Jan. 2	-0.68	Apr. 3	-0.62
9	-0.63	10	-0.44
16	-0.63	17	+0.06
23	-0.54	24	+0.51
30	-0.54	May 1	+1.01

To sum up, while the growing season of redwood in Monterey County appears to approximate the period April-October, it must be borne in mind that many variations occur dependent upon the individual site factors, the character of the seasons and the condition of the tree. Continuous growth in redwood has not been disclosed by the dendrographic studies.

For other species than Monterey pine and redwood, the dendrographic studies are insufficient in number to form the basis of detailed analyses of the period of diametral growth. The following summary statements are therefore merely indicative. Except as otherwise mentioned, the observations refer to trees growing in Monterey County, within 19 km. of Carmel, some native, others planted.

The tendency toward continuous growth of the evergreen Monterey cypress has already been discussed (see table 10).

Deciduous trees are likely to experience shrinkage when in a leafless condition. For a bigleaf maple, accordingly, the period of net growth in 1932 extended from mid-June to early August (fig. 15). An arroyo willow did not begin its 1922 growth until the first of May at the earliest. Inasmuch as the total amount of the preceding hiemal shrinkage is not known, it is probable that the beginning of effective growth was yet later. Growth was not fully terminated before the first of October.

In Arizona walnut at Carmel the diametral increases may cease as early as the first half of July (fig. 9) or as late as mid-November. In five years it was between mid-April and the end of May that the tree reattained the diameter it had had the preceding summer or autumn. In the year 1929, Arizona walnut No. 1 apparently failed to experience a net increase. While diametral increases occurred during the spring and summer months they were insufficient to cancel, by the first of July, the shrinkage which had begun the preceding August. The record for one week in July 1929 is obscure. The autumnal shrinkage for 1929, however, began in mid-August, and it is clear that if there was any net increase for the year it could not have been very great.

While the bald cypress is not fully deciduous at Carmel, yet a short dendrographic study indicates that the season's growth is terminated at about the time the leaves start to fall and begins again when the leaves are fully grown (fig. 14).

The growth period of the MacDougal cottonwood in southern Arizona extended in one year (1932) from about the middle of March to about the middle of October, with hiemal shrinkage during the preceding and following leafless periods.

The essentially evergreen coast live oak may suffer seasonal shrinkage in dry weather (fig. 14), but otherwise the growth does not seem to be limited by seasons. A planted whiteleaf oak (No. 2), on the other hand, appeared to have a program approximating that of a deciduous tree, with an interval of hiemal shrinkage. The period of trunk enlargement (exclusive of cancellation of winter shrinkage) extended at Carmel in 1931 from the first of May to the first of August. After this, dry-weather shrinkage was effective (fig. 9). This is especially notable in view of the fact that the

tree, like coast live oak, retains the old leaves until those of the next year's suit are well developed, or about 13 months.

California laurel and palo verde present curious cases. At the end of one year of dendrographic study (Oct.-Sept.) a tree (No. 1) of the former species was definitely smaller than at the beginning (fig. 15). Sustained diametral increase, as opposed to shrinkage, began early in April, but it was not until mid-July that the winter's shrinkage was canceled. After seven weeks, the diameter was again smaller than at the beginning. The growing season for this species is therefore very hard to delimit on the basis of this brief study.

The performance of the palo verde is even more anomalous. As has been mentioned, a tree of this species 1 dm. in diameter was 3 mm. smaller at the end of four years than at the beginning of the dendrographic study. While this shrinkage was not uninterrupted, yet the periods of diametral increase were not of such a nature that they could be regarded as indicating a definite growing season. In only one case do the records show diametral increases for as much as four consecutive weeks. This occurred in September and October 1929. Other periods of enlargement extending through 1 to 3 weeks have occurred in every month of the year, with no definite concentration of distribution.

It would be difficult to state with assurance the extent to which this tree has been subjected in the past to such unfavorable environmental conditions as those of the past four years. Certainly these conditions have allowed of growth at some time or other. It is, however, quite possible that the tree's growth has been much interrupted by unfavorable periods like the present. It is extremely probable that the time taken for the tree to reach its present size is much greater than might be supposed from a casual inspection.

LEAF DEVELOPMENT AND DIAMETRAL GROWTH

The times of beginning of diametral growth in the spring and of enlargement of the leaves are not necessarily the same. The reports of a number of workers, based on studies by various methods, indicate that the greatest diversity is to be expected in this relation as between different species or different localities or different seasons. These findings have been summarized by Lodewick (1928, 11-13) and it is unnecessary to review them in detail here. Suffice it to say that it has been found that increase in diameter sometimes begins before the opening of the leaves, sometimes coincidentally with this, and sometimes only after the leaves are partly or fully grown.

Lodewick (1928, 47) reached the conclusion that the occurrence of xylem increments at the time of bud opening, or just before, was a characteristic of species with ring-porous wood. Coster (1927, 38, 32), however, remarks: "The phenomenon, which has been so frequently observed in Europe, that growth in thickness begins even before the buds have unfolded, I have not met in the tropics." It was suggested by Knudson (1913) that diametral increase in European larch reported by Buckhout (1907), on the basis of steel tape measurements, as beginning at the same time as leaf formation was very probably "due mainly to a swelling of the tissues."

A comparison of this relation in trees of different types is given in a paper by Hastings (1900). Here it is reported that in the case of broad-leaved trees studied in the vicinity of Ithaca, New York, "no increase in thickness took place until the buds had opened and the first leaves expanded." The angiosperms examined were of the following species: *Acer negundo*, *A. rubrum*, *Quercus velutina*, *Salix fragilis* and *Tilia americana*. A similar state of affairs was found in the case of *Taxodium distichum*, a deciduous gymnosperm, regarding which the author states: "No growth in thickness begins till the leaves are expanded. . . ." Of *Pinus strobus*, on the other hand, he writes that "increase in thickness began on 2 and 3 year twigs before . . . the buds had opened."

These studies of Hastings were based on microscopic examination of wood cut from the trees at intervals during April, May and June. The dendrographic studies of diametral increase indicate a somewhat similar relation of this expansion to the time of leaf enlargement.

In the case of Monterey pine, growth begins long before the leaves of the current year have attained their full size. Although detailed measurements of leaf growth are not available for the Monterey pines of which dendrographic studies have been made, some significant comparisons can be made. Monterey pines Nos. 1, 28 and 31, for example, were increasing steadily in diameter by the end of January or the first of March 1931 (fig. 9). These trees stood in a long row, two of them 6 dkm. apart, the other about halfway between. Some of the leaves of the current season on trees situated on approximately similar sites as these three, however, did not reach full size until after the first of June. It is a fair assumption that the same was true for Nos. 1, 28 and 31, the trees with the dendrographs. By this time, however, these three were definitely diminishing in diameter. During the development of the new leaves on Monterey pines, two or three old suits of leaves are commonly still on the tree, and it appears that these are able to supply the building materials which go into wood production. Similar conditions prevail in the redwood, diametral growth starting before the current year's leaves have attained full size. The same appears to be true for ponderosa pine and Douglas fir, as well (MacDougal, 1921,¹ 29, 30).

The majority of deciduous broadleaved trees of which dendrographic studies have been made have not been found to exhibit diametral increase until after the leaves are at least partly grown. MacDougal (1921,¹ 37; 1924,¹ 50-51, 56, 57; 1924³) and Korstian (1921) have reported such a relation for beech, boxelder, Arizona walnut, both a native tree in Arizona and a planted tree at Carmel, two species of *Populus*, arroyo willow and a sycamore.

A dendrographic study of bigleaf maple (No. 1) in 1932 indicates that in this species diametral enlargement can not be expected until after the leaves have attained full size. The buds of this tree began to open about March 14 and the leaves were full size by April 4; steady diametral increase did not begin, however, until the middle of May. This tree was growing in an open stand of moderately large redwoods in Rocky Creek canyon, on a steep slope with northerly exposure. It was 17 cm. in diameter

at breast height and stood about 13 meters high. The dendrograph was attached 12 dm. above the ground with the contacts seated on the outside of the smooth bark, 0.5 cm. in thickness. The age was around 40 to 50 years. It should be noted that on a larger tree of this species 12 dkm. distant, situated in the stream bottom and receiving considerably more direct sunlight, the leaves of the 1932 suit began to unfold as early as December 1931.

On the other hand, it has been noted that a velvet ash and a bagote, growing in Arizona, showed enlargement of the trunks before the opening of the leaf buds (MacDougal, 1924,¹ 53, 55). This observation in regard to ash agrees with reports by other workers. Hanson and Brenke (1926, 301) state that *Fraxinus campestris* "formed new xylem before the leaves had started to expand or the branches to elongate." Their studies were made of cut trees. Lodewick (1928, 16, 21) reports cambial activity in *Fraxinus americana* beginning coincidentally with bud opening or just before. Chalk (1930, 13) states that in no ash trees "does leaf formation precede cambial activity in the stem." To be contrasted with these observations is the performance of a tree of *Fraxinus americana* (No. 1) growing in the lower garden at the Coastal Laboratory. The dendrographic record of this tree, begun in the spring of 1933 before the leaf buds opened showed that diametral increase (aside from rehydration) did not take place before the leaves were fully grown.

I have dwelt upon the relations between leaf opening and diametral increase which have been found to obtain in deciduous angiosperms of several types and in evergreen gymnosperms. What, now, is to be expected with deciduous gymnosperms and with evergreen angiosperms?

Taking up the former first, one brief series of observations has been made on bald cypress, a deciduous gymnosperm rather closely allied to redwood. For this purpose there was used a small nursery-grown tree (No. 1) planted on the grounds of the Coastal Laboratory in the autumn of 1931. When the dendrographic record was begun in mid-February this tree was 10 dm. high and 11 mm. in diameter at the height of the contacts, 4 dm. above the ground. Most of the leaves had fallen, and of the few remaining about 200 were green and 50 half green. The buds had been swelling for several days. During the preceding couple of months the land about this tree had been filled with flood-borne sand to a depth of 25 cm., and in the middle of February the roots of the plant were still under water. While the leaves of this tree had reached their full size about the first of April, and while the leader was elongating actively during the middle of this month, it was not until June that sustained increase in diameter began. In figure 14 are presented graphs showing the seasonal course of diametral changes in this bald cypress tree, as well as those in a nearby pine, walnut, redwood and an oak. The first four of these were all growing in the lower garden at the Coastal Laboratory, the oak standing 8 dkm. distant from the others and 18 meters higher.

As examples of evergreen angiosperms, there are available records for two species of oak and for California laurel. The oaks hold their leaves for about 13 months, the leaves of the preceding season falling shortly after

the new leaves appear. The leaf fall of the California laurel is more like that of pines and redwoods in that the trees may retain their leaves for 4 or 5 years, losing approximately one season's crop each year (Jepson, 1910, 246).

For the coast live oak, native at Carmel, MacDougal (1921,¹ 31) has observed that trunk enlargement began in 1920 about a month after the appearance of the new leaves. The other species of this genus studied at the Coastal Laboratory was whiteleaf oak, native to Arizona, but growing at Carmel. The subject of the investigation (No. 2) was a plant 4 meters tall and 5 cm. in diameter at the height of the dendrographic contacts (7.5 dm. above ground). An instrument was attached to this tree toward the end of December 1930. In the spring of 1931, the leaves of the tree began to unfold about the first of April. Sustained diametral increase started shortly afterward. In view of the fact, however, that there had been considerable shrinkage during the preceding months, there would seem to be a possibility that part of this increase was due simply to rehydration. Mathematically considered, the shrinkage which took place between January 19 and April 6 was not fully canceled until after the 27th of April (fig. 9). At this time the new leaves were nearly half size and many of the old leaves were still persisting. It may be, therefore, that actual cell multiplication and enlargement can not be considered to have taken place until after the new leaves had reached an appreciable size.

To be contrasted with the performance of this oak is that of a 13-cm. Monterey pine (No. 33) and of a 6-cm. planted redwood (No. 18) growing in the same vicinity. As has been seen from table 10, this pine was increasing in diameter as early as January and February 1931. The dendrographic record of the redwood was not commenced until early in February 1931 and the amount of any preceding shrinkage there may have been is accordingly unknown. Before the middle of March, however, enlargement was well under way, and this continued almost without interruption through the summer. Active branch elongation was not evident before the end of April.

The California laurel (No. 1) which was chosen for dendrographic study was one of a clump of nine standing on a slope with northerly exposure, the south wall of Rocky Creek canyon. The tree used was 18 cm. in diameter at the contact points 13 dm. above the ground, and about 10 meters high. It stood nearly erect. Most of the other trees in this clump were smaller. The age of one of them, which was 16 cm. in diameter and cut during the time of the dendrographic study, was about 50 years. It seems likely that all the individuals of this group originated as sprouts at about the same time and possibly subsequent to a severe fire. The dendrographic contacts were seated on the outside of the smooth bark of the tree.

The dendrograph was maintained in operation on California laurel No. 1 from September 1931 to December 1932. Growth took place during a comparatively short period, and the net diametral change recorded was a decrease. The chief diametral increase for the year began at about the time the leaves unfolded and before they had attained more than one-third

their full size. In figure 15 the changes for a 14-month period are shown graphically, together with those of bigleaf maple and redwood for comparison. All these trees stood within 0.6 km. of one another.

From the facts just presented it would appear that in the case of the two oaks which hold their leaves a little over a year, diametral increase is hardly to be expected before the new leaves unfold and that there is some evidence to indicate that they must be at least partly grown before diametral growth can take place. Even in California laurel with its long-persisting leaves, it does not appear that diametral growth can take place prior to the partial development of the new leaves. These evergreen broad-leaved trees, in other words, approximate the spring program of deciduous trees, gymnospermous as well as angiospermous, rather than that of the evergreen conifers (figs. 9, 14, 15). No detailed anatomical or physiological examination of these persistent angiospermous leaves was made in connection with these studies. It seems possible, however, that the conditions which are responsible for the formation of absciss tissue in deciduous trees may also be responsible for an interruption in the conducting elements, whereby the elaborated food substances are transported from the leaves to the cambium. It seems that the leaves, although still green, can not function effectively in supplying food for the growing tissues in the lower parts of the tree.

TABLE 14—*Effect of defoliation on diametral growth, Monterey pine.*¹

Tree No.	Diametral Changes	
	Dec. 31, 1923 to June 30, 1924	Dec. 29, 1924 to June 29, 1925
23 (defoliated Aug. 25-27, 1924)	mm. +6.0	mm. -0.1
6 (control)	+4.2	+13.6

¹ The plus sign indicates a diametral increase, the minus sign a diametral decrease.

From the foregoing considerations, we can say that while definite exceptions have been reported, it appears that the food elaborated by the developing leaves of deciduous trees and of some evergreen broadleaved trees is in many cases used largely or exclusively for their own growth and that of the new twigs until the leaves have attained a third or more of their full size. Possibly that produced by the new leaves in a pine tree or other evergreen conifer also goes to their own development. This last supposition is supported by observations on the effects of defoliation of evergreen coniferous trees.

MacDougal's defoliation tests have shown that "removal of all green leaves from a Monterey pine in the resting-period or in winter results in its death within a few months" (1925,¹ 89). This was found to be the case when defoliation was performed in January (No. 27) or in October (No. 25). When the old leaves were removed from a tree in March (No. 19), May (No. 29), June (No. 23), or August (No. 23) death did not ensue. At the time of the March defoliation, the new leaves were about

half grown. This defoliation was followed by a markedly reduced rate of growth, but not by death of the tree. Removal of the old leaves in June (No. 23) seemed to have no effect on the progress of diametral enlargement (MacDougal, 1924,¹ 26). In the year following August defoliation (No. 23), the growth of the experimental tree was characterized by a marked reduction as compared with the previous year (table 14).

LOCALIZED CAMBIAL ACTIVITY

Many investigators have reported that the period of cambial activity may be quite diverse in different parts of a tree. These studies have had to do mainly with the relatively orderly progress of growth initiation and cessation in the tree (cf. Lodewick, 1928, 8-10). Observations of Coster (1927), however, suggest that under certain conditions the cambial activity may be quite erratic. He reports (38, 108) that exotic broadleaved trees in western Java often showed a periodicity of leaf fall by branches, as a result of which the tree was never without green leaves. A beech tree (*Fagus sylvatica* L.), for example, is described as always presenting about the same appearance: part of the crown dormant, with dry, brown, persisting leaves; individual smaller branches bare, with dormant buds; a few elongating branches with unfolding leaves; and still other branches carrying green full-grown leaves (37, 140). In the case of bald cypress (*Taxodium distichum* Rich.), which is winter-deciduous in its native habitat, the cambium seemed always more or less active although there was great variation in the stage of wood-formation on different parts of the tree (37, 132-133). It appears that during the leafless period of a branch, the cambium of that branch was dormant (38, 29). MacDougal and Working (1933, 81) report that localized cambial activity is to be expected in palo verde.

The records of the two instruments on Monterey pine No. 1 (fig. 21) show that in general there is a definite parallelism in diametral changes at the two heights. For the most part, when the tree was increasing in diameter 1 meter above the ground, it was also increasing at a height of 8 meters. Conversely, shrinkage at the top and bottom usually occurred simultaneously, or nearly so. The differences recorded are largely of degree. In 1927-28, for instance, the shrinkages and swellings occurred at much the same time at each height, but the summer growth at 8 meters was appreciably less than at 1 meter and the following autumnal shrinkage was much greater. A few erratic shrinkages seem to be coupled with resetting of the frame and were probably caused by a slight drying out of tissues exposed in preparing seatings for the contact rods. It is also to be noted that in some 12-month periods, diametral growth at the upper instrument is less than that at the lower (for example in 1927-28), whereas in other seasons the reverse is true (1926-27). This individual is a dominant tree in an open stand; and there is no obvious explanation of these differences and other minor irregularities.

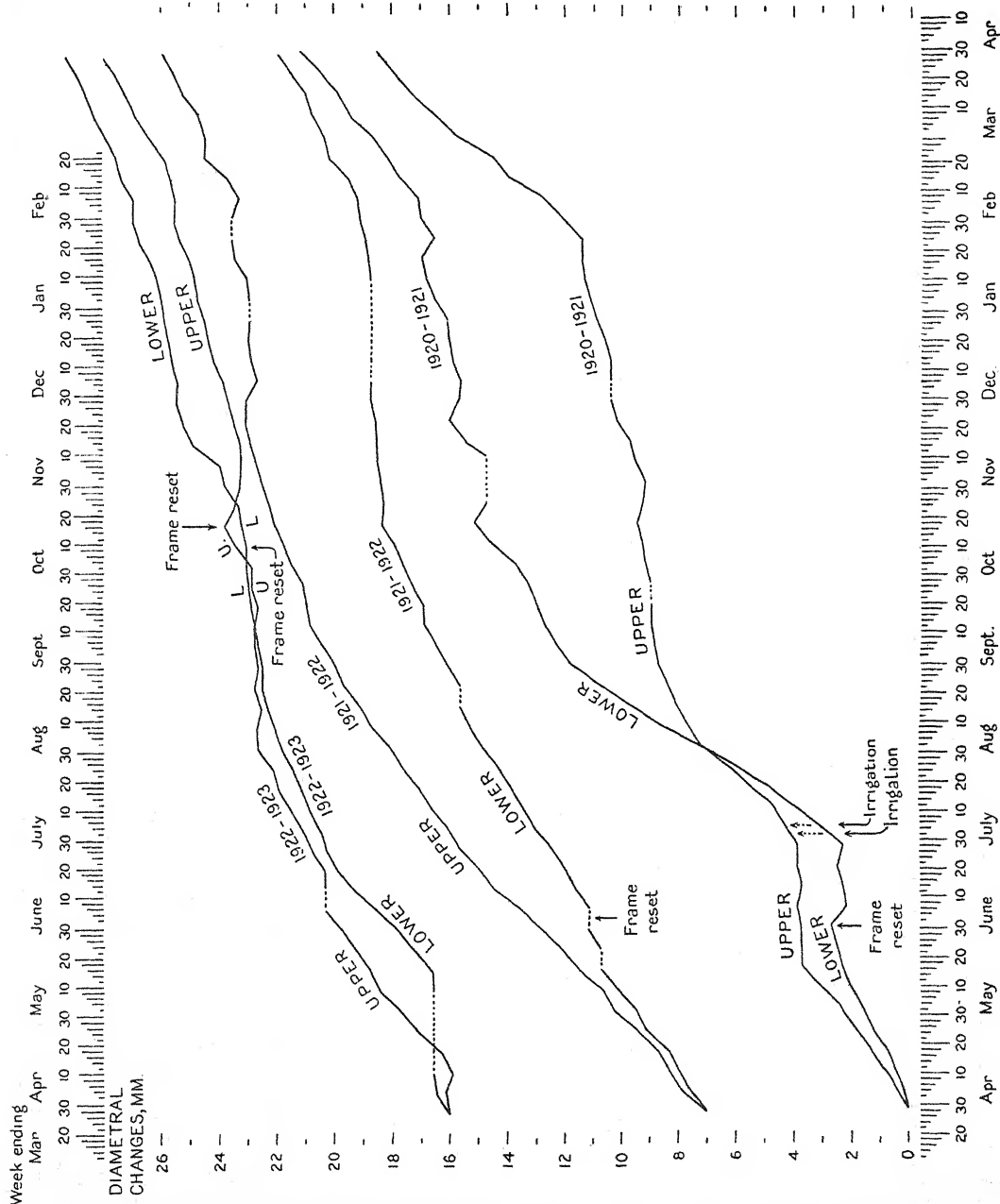
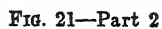
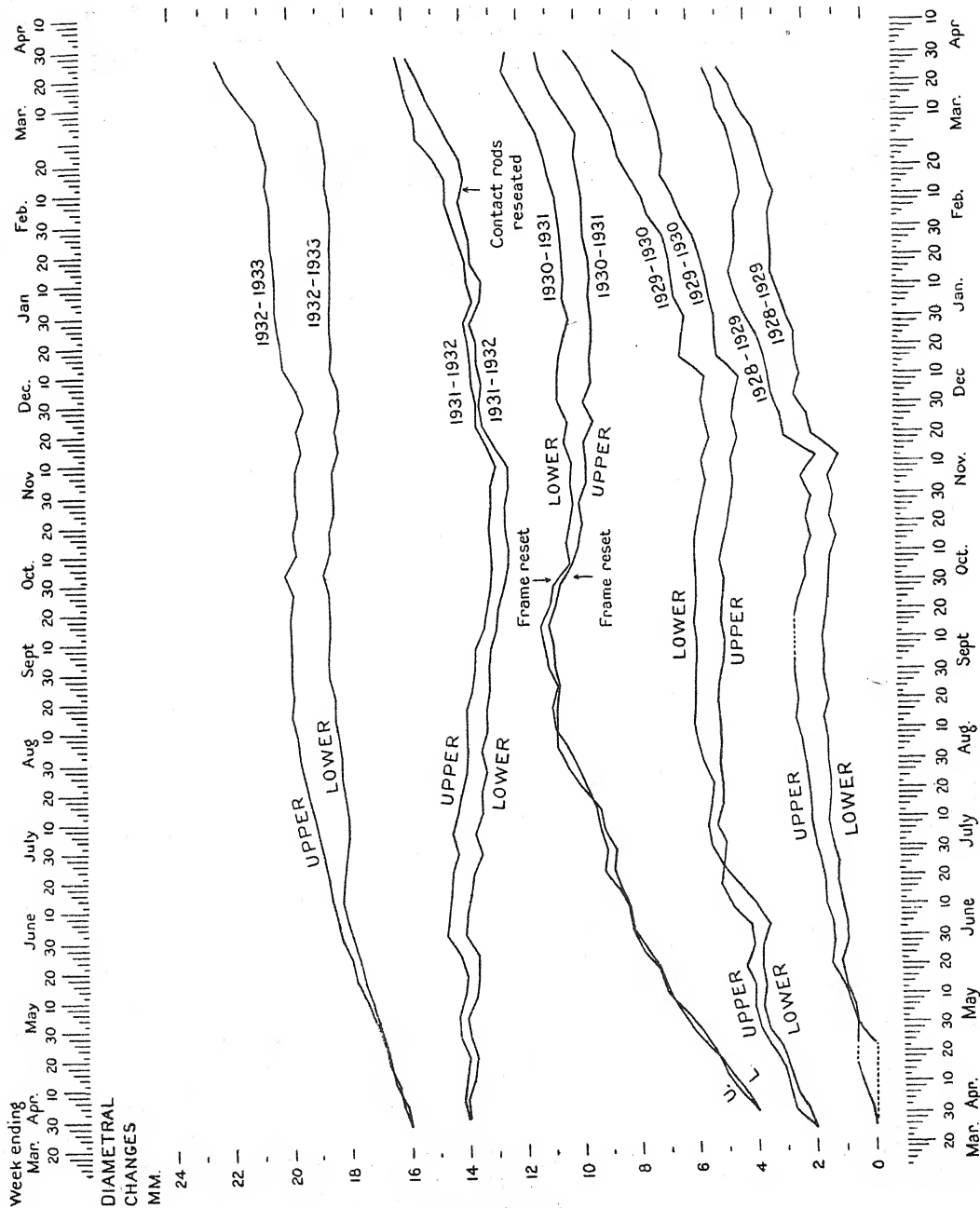


FIG. 21.—Diametral changes for Monterey pine tree (No. 1), week by week, for thirteen years. This tree carried two dendrographs, the lower (1-A) at height of 1 meter above ground, the upper (1-B) at height of 8 meters above ground. Cumulative weekly changes are plotted from arbitrary starting point for each year, zero point for both graphs being same. Records are given for annual period beginning on Monday about April 1. Dotted graphs indicate missing records. It will be seen that while there is a general similarity between the two graphs for each season, there is no uniformity in their relations to one another: sometimes upper part of tree grew faster than lower, while at other times the opposite was true. Seasonal shrinkage is illustrated for a number of years, and effects





EFFECT OF GIRDLING ON DIAMETRAL GROWTH

Mechanical girdling of a Monterey pine tree during the growing season (May) resulted in reduction of the rate of enlargement, but did not appreciably affect the length of the growing season that year (MacDougal, 1924,¹ 13-14). In the case of a redwood (No. 16) girdled in July (as described in the Section on Diurnal Fluctuations) the rate of diametral increase was at once materially reduced as is shown by comparison with a nearby control (No. 6). These relations are illustrated in figure 22.

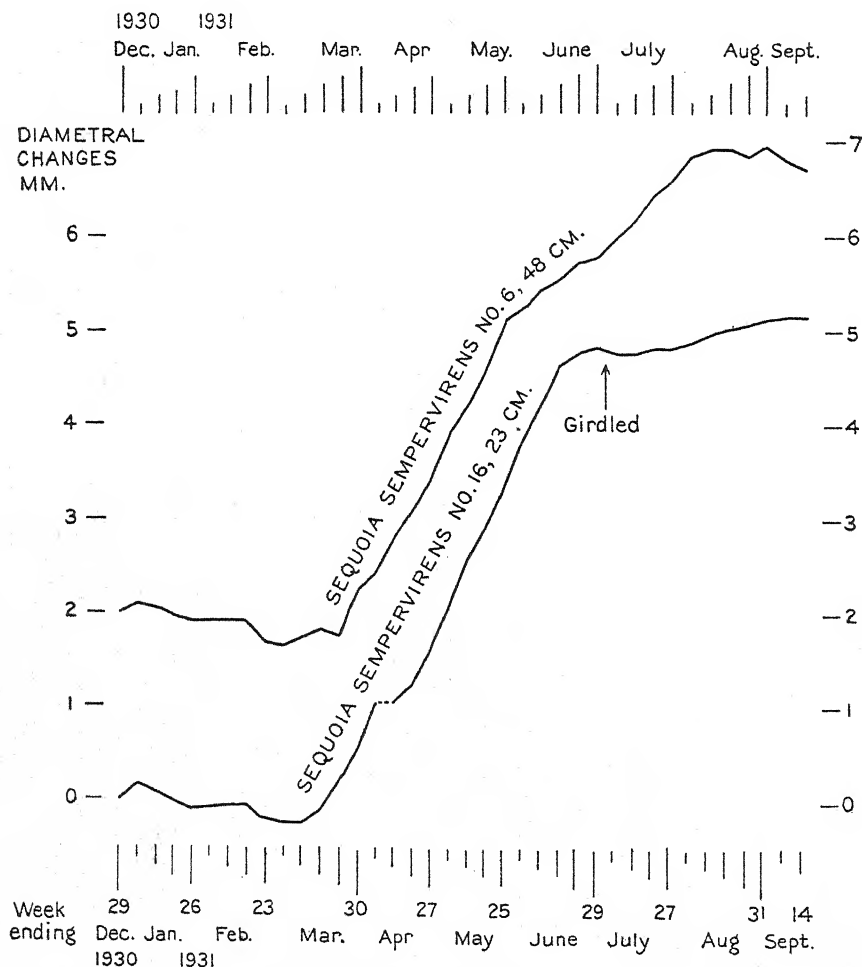


FIG. 22—Effect on growth of girdling a redwood tree. From arbitrary starting points cumulative changes in diameter week by week are shown for experimental tree (No. 16) and for control (No. 6). Prior to girdling, progress of diametral changes in two trees had been essentially same. Both trees were growing at time girdling was performed. Subsequent to girdling, growth in experimental tree promptly fell off. Dotted graph indicates missing record.

SIGNIFICANCE OF DIAMETRAL CHANGES

In the foregoing sections, the object has been to present a summary of the facts observed in the course of dendrographic studies of tree growth, which have to do with increase and decrease in diameter of tree trunks. With these have been included some critical comments on the recorded facts. We have now for consideration a more detailed analysis of the significance of these changes from the standpoint of the physiology of the tree.

LOCATION OF FLUCTUATION

We may begin this analysis with an inquiry into the regions of the tree in which occur the reversible variations in diameter. It is to be kept in mind that as the dendrograph is generally set up, the diameter under observation includes wood, cambial elements and a layer of the outer tissues. The diametral changes are obviously the net sum of all changes occurring in all the elements situated between the two contact points. As will appear presently, the investigations of diametral changes in woody cylinders indicate that the seat of the greater part of the observed changes in a tree must lie outside most of the wood itself. It might well be asked whether any large part of these changes is ascribable to loss of moisture from the bark direct to the adjacent air or, to the converse, absorption of moisture from this air, or from water running down the bark itself. The results of several experiments help to answer such a question.

In one of these experiments two dendrographs were operated on one tree (No. 6) of Monterey pine for a period of a few weeks. The frame of each of these two instruments was built up of six pieces of Permament steel. The magnification in both cases was 22 times; and, in general, an effort was made to have the two instruments similar except for the seating of the contact rods. For one instrument (No. 6) these rested on bark which had been pared down to a thickness of 1 or 2 mm., while those of the other instrument (No. 6-A) were set on the intact bark, which was 2 cm. thick. The instrument with contacts on the outside of the bark was set 19 dm. above the ground. It was somewhat above the other, the contact points of the two being 7 dm. apart. The diameters measured made an angle of about 15° with one another. The weather during the period of study in January and February 1931 included both clear and overcast skies, with occasional showers and some markedly windy days. Temperatures varied from 4° to 30° C. (39° to 86° F.).

Although the graphs obtained with these two instruments are not identical, they show a surprisingly close agreement, as is exemplified by those for the week of February 9-16, 1931, here reproduced as figure 23. During this week there were a number of showers, mostly light, and interspersed with some periods of clear weather. It will be seen from figure 23 that these dendrograms ran very nearly parallel. The diurnal fluctuations were almost identical day by day for the two, although there was a slight difference (0.3 mm.) in the net weekly change.

It seems likely that if absorption of atmospheric moisture is a significant cause of the observed diurnal fluctuations, then the instrument with con-

tacts on the thicker bark would record greater variations than the other. No pronounced difference of this sort appears in the dendrograms. Another possibility is that the intact bark might be more resistant to wetting than the cut bark. In this case the cut bark would be expected to experience greater fluctuations in thickness than the other. Here again, however, the dendrograms do not show such a difference.

As another experiment, the bark of a Monterey pine tree (No. 20) was artificially moistened under the contacts of its dendrograph. This experiment was performed in December 1930 after a period of 10 days without rain. No unusual increase in diameter resulted from this treatment.

Further evidence along these lines is afforded by the results of irrigation experiments with Monterey pine. As will be seen by reference to figures 12 and 13, the diametral swelling in this species following irrigation is very similar to that following rain, in spite of the fact that in the former case the atmospheric humidity is not appreciably increased. The fact that an increased amplitude of daily fluctuation has been observed to follow irrigation as well as rain also indicates that absorption of atmospheric moisture by the bark can not be the chief factor involved (figs. 1, 13).

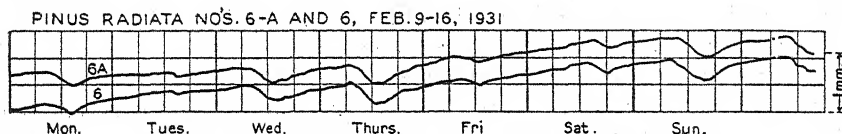


FIG. 23—Dendrographic records made by two instruments on one tree, illustrating relative insignificance of bark thickness in dendrographic studies of Monterey pine. Instrument No. 6 had its contacts seated on bark which had been pared to thickness of about 2 mm., whereas contacts of No. 6-A were resting upon intact bark, 2 cm. thick. Note diurnal fluctuations and general course of growth as recorded by two instruments were essentially the same.

It seems evident from the above cited observations that loss of moisture from the bark direct to the air and absorption of moisture by the bark from the air, or from free water on its surface, can be held responsible for only an insignificant part of the reversible changes in diameter of pine trees.

In the case of coast live oak, however, it appears that the amount of moisture in the air or on the bark may be of somewhat more significance as a cause of shrinkage and rehydration. Although the swelling in the bark which follows irrigation of this species is very prompt, it is likely to be less abrupt than that occurring after rain. It is to be noted that subsequent to a moderate rain, the swelling has been found to take place in the bark of this species rather than in the wood. This relation is illustrated in figure 5. Irrigation, however, was followed by swelling of the outer layers of wood, as well as of the bark (fig. 18).

Another aspect of these water relations is also illustrated by figure 5. Although the immediate response to rain was greater in the entire tree than in the woody cylinder, yet the net increase for the week was greater in the entire woody cylinder (No. 3-B) than in the wood with its surrounding

bark (No. 3). The following week, which was rainless, the tree as a whole experienced a definite shrinkage, whereas the woody cylinder increased in diameter (fig. 24). It will be evident from an examination of figure 24 that the diametral contraction of the bark during the week indicated must have been the *sum* of the *decrease* recorded by dendrograph No. 3 (for the entire tree with bark) and the *increase* recorded by No. 3-B (for the woody cylinder without the bark). This totaled (0.23 mm. + 0.31 mm.=) 0.54 mm.

Recent experiments by Doctor MacDougal, in which freshly cut stems were stepped in an aqueous solution of acid fuchsin, failed to show that the dye could cross the cambium from the wood to the bark. Neither did the dye enter through the outer epidermis of bark which was immersed in the solution.

Doctor MacDougal also found that cubes of oak bark, 20 mm. on a side, cut in June and immersed in tap water, swelled 1.5 per cent when cut after a period of dry weather, but only 0.6 per cent when cut after the trees had been subjected for 14 hours to a light drizzling rain. This relation suggests that water is absorbed by the bark during periods of wet weather. Nevertheless, sprinkling the bark of a living tree of coast live oak (No. 4) with water in August did not result in any marked swelling.

Some years ago MacDougal (1925,¹ 3) reached the following conclusion: "The facts given in . . . this paper establish beyond all doubt that the daily reversible variations in the trunks of trees are intimately linked with the course of transpiration and with the daily stomatal program." Elsewhere (1926,¹ 124) he has noted that "upwardly moving columns of water in the Monterey pine occupy the layers connected with the leaves." His studies showed that "The wood of the terminal internode and of the second, third and fourth layers of older nodes [was] so connected."

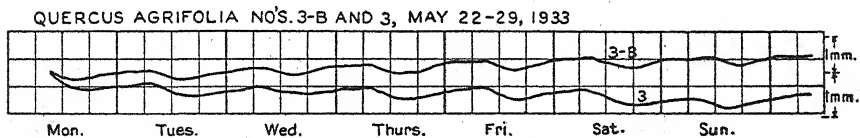


FIG. 24—Dendrograms illustrating shrinkage of bark of coast live oak while woody cylinder of same tree is increasing in diameter. Total contraction of bark during week indicated is sum of decrease recorded for entire tree with bark (No. 3) and increase recorded for woody cylinder without bark (No. 3-B).

In view of these observations it is rather surprising to find the relatively small amount of fluctuation occurring in the woody cylinder of a 25-cm. Monterey pine (No. 20) as compared with that in the entire tree. The dendrographs with which these comparisons were made were attached to the tree about a meter apart, the one (No. 20-C) for the woody-cylinder records above the other (No. 20). The diameters whose changes were measured by the two instruments lay in the same vertical plane. The contacts of No. 20-C were on faces about 4 cm. square from which the bark and cambium and a layer of wood 1 or 2 mm. thick had been cut away. They were therefore on wood formed during the early part of the current

season or in the preceding season. The bark layers under the contacts of instrument No. 20 were about 1 to 2 mm. thick.¹

Representative diurnal fluctuations for this tree and for the woody cylinder alone are shown in figure 25, while in table 15 is presented a comparison of the weekly changes in the two cylinders. The maximal difference between the diurnal fluctuation recorded for the entire tree and that for the woody cylinder on the same day was 0.474 mm. Inasmuch as the total thickness involved on the two sides of the tree was about 6 mm., there was a diurnal change in this region amounting to 0.079 of the diametral distance (or 1 in 13). Reference to table 2 will show that this is an extraordinarily large ratio. As MacDougal (1925,¹ 5) has pointed out this is an aspect which is not to be ignored in measuring the flow of materials through the tissues concerned.

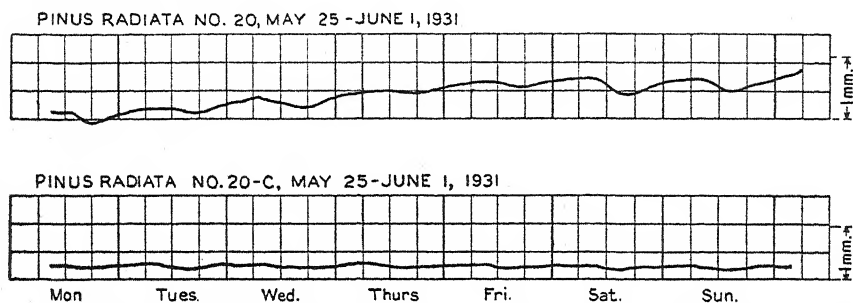


FIG. 25—Dendrographic records for Monterey pine tree showing diurnal fluctuations in entire tree, including cambium and thin layer of bark (No. 20), and in woody cylinder alone (No. 20-C).

It appears from these figures that a very large amount of the daily and seasonal variation in moisture content in a Monterey pine occurs within a relatively thin layer of tissues lying in the vicinity of the cambium. The approximate radial thickness of this layer may be tentatively taken as 3 mm.

The amount of fluctuation in the woody cylinder of a 23-cm. Arizona walnut tree (No. 1) was larger than in this Monterey pine (fig. 6). In the walnut genus the transpiration stream can be expected to traverse "the outer portion of the late summer wood and the innermost portion of early spring wood," but not those zones where tylosing has occurred (MacDougal, Overton and Smith, 1929, 37-38).

With coast live oak, by far the greatest part of the diurnal fluctuations appears to be localized in the thick bark which is characteristic of this species (fig. 24).

A transmission line pole, apparently of incense cedar (*Libocedrus decurrens* Torr.), to which a dendrograph was attached for a couple of weeks in the summer of 1933, showed slight diurnal fluctuations amounting to a maximum of 0.025 mm., or 0.0001 of the diameter. This is considerably less than the fluctuation occurring in the woody cylinder of a living Mon-

¹A more detailed report on this study will be found in a recent paper of the writer's (Haasis, 1933¹).

TABLE 15—*Weekly diametral changes, in millimeters, of a Monterey pine (No. 20).¹*

Week ending	Entire tree (20; including about 2-4 mm. of bark)	Woody cylinder (20-C; bark, cambium, and about 2-4 mm. of wood removed)
1931		
Apr. 27	+0.36	+0.18
May 4	+0.59	+0.13
11	+0.23	+0.08
18	+0.45	+0.03
25	+0.41	+0.50
June 1	+0.68	-0.08
8	+0.59	-0.08
15	+0.36	+0.11
22	+0.27	+0.16
29	0.00	+0.11
July 6	+0.50	0.00
13	-0.05	-0.03
20	+0.18	0.00
27	+0.18	0.00
Aug. 3	+0.36	0.00
10	+0.23	0.00
17	+0.36	+0.05
24	+0.14	0.00
31	+0.32	0.00
Sept. 7	+0.09	-0.03
14	0.00	0.00
21	+0.05	-0.08
28	-0.14	+0.05
Oct. 5	-0.05	0.00
12	0.00	0.00
19	+0.05	+0.03
26	-0.05	-0.03
Nov. 2	+0.05	-0.03
9	-0.41	-0.05
16	+0.59	+0.05
23	-0.09	-0.05
30	-0.05	0.00
Dec. 7	+0.05	-0.05
14	+0.05	+0.05
21	+0.09	-0.05
28	+0.27	-0.13

¹ The plus sign indicates diametral increase, the minus sign diametral decrease.

terey pine. The pole used was 25 cm. in diameter and the contacts were seated on non-weathered wood after scraping off a layer of soft weathered wood less than 1 mm. thick.

The fact that a tree fails to show growth in diameter at a point a few feet above the ground does not necessarily indicate that it is growing at no other point. This is demonstrated in one way by the records obtained with two instruments on the same tree of Monterey pine (No. 1), but 7 meters apart. As will be seen from the accompanying graph (fig. 26), this tree sometimes shrinks at the upper instrument while it is increasing in diameter at the lower, although at other times the reverse is true.

It is not unusual for a plant to increase in length while no diametral increase is taking place. Indeed Pfeffer (1903, 13) states that a diametral

decrease may occur during the period of elongation. This is borne out by dendrographic observations in 1931. A small tree of Monterey pine (No. 31) shrunk appreciably at a height of 3 dm. during the summer and fall of that year (fig. 9) although the tip (11 dm. above ground) continued to elongate. Between March 28 and October 9 this terminal increased 120 mm. in length while the stem decreased 1.6 mm. in diameter. As has been mentioned earlier in this paper, growth at the top may also occur in redwood even though the stem be shrinking. It is obvious that in these trees, as well as in the larger Monterey pine (No. 1), we also have examples of increasing diameter in one part of the stem while another part is decreasing.

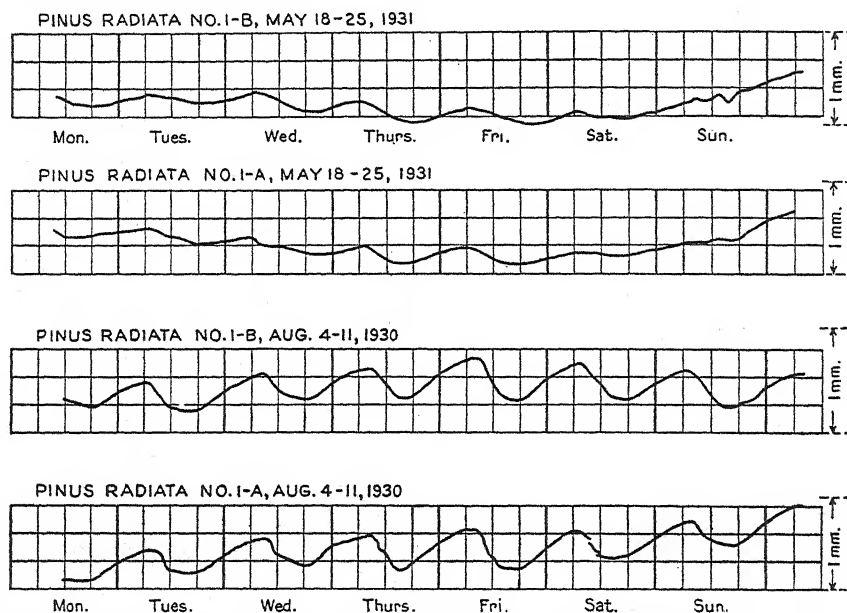


FIG. 26—Dendrographic records made by two instruments on Monterey pine tree at heights of 1 meter (No. 1-A) and 8 meters (No. 1-B), respectively, showing differences in diametral changes at two heights. Note tree sometimes shrinks at lower instrument while increasing in diameter at upper (May 19-20), and vice versa (Aug. 9-11). Diurnal fluctuations are well shown by records for August 4-11.

Observations on a palo verde, in Arizona, indicate that in this species "active growth is localized and a general activity of the cambium over the whole trunk is not the rule" (MacDougal and Working, 1933, 81).

These observations are much in accord with those of several earlier writers. Fritz and Averell (1924), for example, have found instances of local inactivity, for many years, of redwood cambium on one side of a tree while growth was taking place on another side. Huntington (1928) records for bigtree (*Sequoia washingtoniana* Sudw.) differences of as much as 20 or 30 growth rings on radii lying at right angles to one another; and indeed an extreme difference of 500 rings on opposite sides of a 3000-year old tree (p. 14). Hartig (1870) reported the complete suspension of ring-formation in the lower part of the bole of suppressed trees. Bailey (1925) refers to

cambial inactivity in the lower part of a tree bole for several years following defoliation by insects, whereas this suppression did not occur in the apical portions of the stem. For *Peltophorum ferrugineum* Benth., a species of the Leguminosæ, Coster (1927, 37, 88; 38, Pl. I) reports that the growth rings of trees from western Java are sometimes absent for part of the periphery. This author in fact found many cases of very pronounced localization of growth. In this connection there may be mentioned, too, the observation of Tumanow (1930) that in many plants in a wilted condition the water deficit is distributed very irregularly through the individual and that individual organs can sustain life at the expense of other organs. While Tumanow's studies were made on various grains and legumes, it seems entirely likely that similar differences would be found in a large woody plant and, indeed, to an even greater degree.

Before the development of his dendrograph, MacDougal (1918¹) made the following comments on the conditions obtaining in the stem of an annual dicotyledonous plant: "There exists a state of affairs in a growing sunflower stem by which the extreme terminal portion will be found in a condition of continuous enlargement, the internode below will show daily shrinkages or cessation of growth in thickness . . . , while the internodes below will show even greater variations in volume. The older parts of the stem consist very largely of mature tissues which take up and give off water in a manner entirely reversible, and in organs or members in which the embryonic tissue is reduced to a minimum, the widest range of reversible alterations occurs."

RELATION OF DIAMETRAL FLUCTUATION TO LIQUID TENSION WATER CONDITIONS IN A TREE

Before taking up a consideration of the relation of diametral fluctuation to liquid tension, it will be well to fix in mind as clear a picture as possible of the distribution of water in the tree. Our understanding of this has been much advanced by the experiments of MacDougal and his associates (MacDougal, 1926,¹ MacDougal *et al.*, 1929, 1933), a detailed analysis of the relations involved has been presented by Livingston (1927¹), Hawley (1931) has published a synopsis of some of the physical aspects concerned, largely from the viewpoint of drying wood and of impregnation with preservatives, and Woodhouse (1933) has recently prepared a comprehensive summary of contributions on this subject. Reference is made to these publications for a fuller discussion of the matter than is given in the following sketch.

The outermost part of a tree (within the bark) consists of a layer of living cells, containing a relatively large amount of water. Interior to this zone is found a region of older woody tissues, more or less occupied by a mass of water (or more strictly aqueous sap) under greater or lesser tension. The innermost tissues are for the most part gas-filled, but the localization of gas and sap within the tree trunk exhibits the greatest diversity, both between species and from time to time in an individual tree. There may be occasional strands of water within the main gas mass, or isolated gas-filled elements within the main water mass. Sometimes layers of gas-filled

tissues are intercalated between successive layers of sap-filled tissues. The liquid layers, however, are not discontinuous, but are joined into one connected whole, although some of the parts of this may consist of exceedingly narrow and elongated filaments. The liquid mass is also continuous with the sap of the zone of living tissues.

The mass or meshwork of sap (or water) under tension occupies woody tissues and has roughly the shape of an elongated hollow cone with conical ramifications extending into the branches and twigs, terminating in fine divisions in the leaves, and similar projections reaching down into the roots from the base of the cone. It fills the lumina of fine-bored woody conduits and saturates their walls, maintaining its position by virtue of the imbibitional forces in the walls and the cohesion between the water molecules.

At the uttermost extensions of this water mass in the leaves, evaporation takes place from minute terminal water surfaces, or menisci. As this water is evaporated, or transpired, more is drawn up to the terminal points. The water moves as liquid strands or wires through conduits whose walls are filled and faced with water. It may be, as suggested by Kramer (1932) and Woodhouse (1933), that these liquid strands are continuous through the roots and into the soil when transpiration is rapid.

Changes in the liquid water content of the various parts of a tree are occurring constantly. They are dependent in the main upon the water content of the air and its temperature and rate of movement, upon the physical and chemical character of the soil and its moisture content, and upon material changes occurring in the plant itself with the fixation or release of water. As transpiration takes place from the water menisci in the leaves, the water strands are subjected to tension. Although these strands are able to resist a very considerable pull (because of the forces of cohesion in the water), with intense transpiration some of them will become ruptured and the conduits filled with gas. Generally speaking, those water strands in the largest conduits will be the first to break. Such an occurrence in a few conduits, however, need not affect conduction through the meshwork as a whole, any more than the breaking of one or two cords in a fish net seriously affects the entire net. Just after rupture of a water strand, the walls of the duct still contain considerable moisture. This is lost only very gradually.

When the tension on the liquid meshwork is removed, as by an increased atmospheric humidity, the sap will gradually (by imbibition and capillarity) move from conduits which are still water-filled into the walls of adjacent gas-filled ducts; and in time the lumina of these ducts may again become filled with sap. Metabolic water may play a rôle in this, as suggested by Münch (1927), but it does not seem essential. Any available water would serve the purpose. Osmotic and perhaps other forces in the roots help to increase the total amount of water in the hydrostatic system as a whole. Individual conduits may at times be filled with water and at other times with gas.

Cohesion in the water strands is effective laterally, between the moving water molecules and the water molecules attached to the cell walls, as well as longitudinally along the water strands. If the conduit walls were faced

with oil instead of water, the water strands might move more readily because of the lesser mutual attraction between oil and water molecules than between water molecules. They would, however, also break more easily because of the absence of support by the surrounding liquid on the conduit walls.

With the accumulation of dendrographic records, more and more evidence becomes available in support of reiterated statements by MacDougal (1921,¹ 6, 41; 1924,¹ 40; 1925,¹ 3; 1926,¹ 5, 116; MacDougal *et al.*, 1929, 97, 98) to the effect that daily reversible variations are closely connected with the water-balance in the tree trunk; and, indeed, to justify the extension of this concept to other variations than the diurnal fluctuations. Transpirational losses exceeding moisture intake through the roots result in diametral shrinkage whether we are considering a 24-hour period or one of greater length. The fact that removal of the top or of the leaves of a tree has been found to result in a reduction of the amplitude of the diurnal fluctuation indicates a close connection between transpiring surface and reversible variations in diameter. Nor is MacDougal's observation (1926,¹ 77) to be overlooked in this connection that diurnal fluctuations may occur even in a dead pine tree.

INFLUENCE OF EVAPORATING POWER OF THE AIR

The close relation between diametral changes and the evaporating power of the air is exemplified by the reactions associated with changes in wind velocity. It has been shown that in Monterey County marked increase in diametral shrinkage can be expected to result from unusually high winds; and conversely when the wind moderates abruptly, this will be reflected in a reduced rate of shrinkage. Phillips (1931) has reported similar observations in southern Africa. In Monterey County, it was further observed that the inner woody cylinder of a pine tree seemed especially sensitive to changes in wind velocity. Why this should be so is not clear.

The amount of moisture in the air, also, has a more or less definite influence on the character and amount of diurnal changes, as has been referred to in the section on Diurnal Fluctuations. An additional set of observations may well be considered here.

In one notably foggy night in April, a pronounced diametral increase was recorded for several of the Monterey pine trees at Carmel as compared with shrinkages which they had experienced in preceding nights. Presumably this is to be correlated with the greatly reduced transpiration caused by the high humidity. The dendrographic records of the woody cylinders did not show this conspicuous swelling. On the contrary, shrinkage occurred there as in previous nights.

It is possible that at least some of the swelling in the entire trees is attributable to absorption of moisture by the bark from the air. In view of the comparison discussed earlier in this section, however, this seems unlikely. The contact rods on the woody cylinders (Nos. 20-B and 20-C) were seated on bare wood or on a very thin layer of hardened resin, and the adjacent wood of the outer bearings, and presumably of the inner, was covered with hardened resin. It seems likely that this layer of pitch pre-

vented to at least some extent the absorption of air moisture by the wood beneath the contact points. However, the program of diametral change in these woody cylinders was distinctly erratic compared with that of the entire tree (No. 20), and the reasons for the divergencies are by no means clear (Haasis, 1933¹). It may be noted that the dendrogram for the entire diameter (No. 20) had not been showing the nocturnal shrinkages experienced by other pine trees on the dune, presumably because of its somewhat better water supply.

INFLUENCE OF WATER-SUPPLYING POWER OF THE SOIL

The water-supplying power of the soil obviously plays a most significant part in determining the water conditions within the tree and so influences the diametral fluctuations to a material extent. As we have seen earlier in this paper, drying out of the soil is accompanied by a gradual shrinkage of the tree and a reduction of the amount of diurnal fluctuation (figs. 9, 13).

Conversely, when after a period of soil desiccation, additional supplies of water are made available to the roots of an experimental tree, two results are soon apparent on the dendrographic records. First, a diametral increase promptly ensues; and second, the amplitude of the diurnal fluctuations is increased before many days. These effects have been observed for both Monterey pine and coast live oak trees. The first is illustrated by figures 12, 13, 5 and 18, the second by figures 1 and 13.

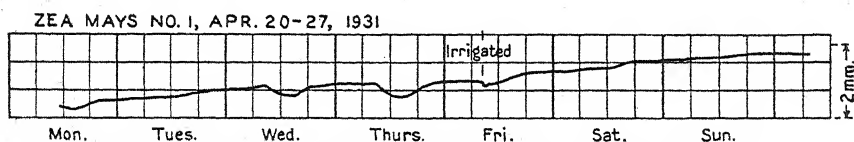


FIG. 27.—Dendrogram showing response of maize plant to irrigation.

Nor are these reactions confined to gymnosperms and dicotyledonous angiosperms with their central pith. Plants of the monocotyledonous genera *Zea* and *Cordyline* show much the same relations to irrigation, as is illustrated in figures 27 and 10. Perhaps in these last-named plants water, when available, is stored in large amounts in the extensive pithy tissues of the stem and later withdrawn from them into the vascular system. This would not be greatly different from the thesis enunciated by MacDougal, Overton and Smith (1929, 10, 99) that there is a constant change in the particular conducting vessels which contain water. It would simply imply a difference in the type of tissue in which storage occurs.

DIURNAL FLUCTUATIONS

Reference has been made in an earlier part of this paper to the time of day at which diametral growth of trees may be expected to occur. We shall now examine these circumstances in a little more detail.

Let us assume a normal tree in healthy condition on a clear day a little after sunrise at a time when the moisture in the soil is plentiful and the temperature, both day and night, is high enough for growth. At this hour the tree will have reached its maximal diameter for the day (fig. 28). Soon

afterward, as the evaporativity of the environment becomes greater, the tree will begin to decrease in diameter. This shrinkage will continue until the intensity of the evaporativity of the environment diminishes, some time during the afternoon, when diametral increase will recommence. It will be several hours before the tree recovers the diameter which it had when shrinkage began. It is not certain that cell division and enlargement, as distinct from rehydration, occur during this interval. Certainly it must be taking place subsequent to this time, during the period when enlargement continues to the next diurnal maximum (13 hr. in fig. 28). Perhaps both growth and rehydration occur throughout the entire period of enlargement (17 hr. in fig. 28). It may even be, as has been suggested by other writers, that cell division can take place during the period of diametral shrinkage. Uleha (1926), working mainly with living pith of various terrestrial and aquatic plants, even concluded that "a certain degree of water deficit appears to be a fundamental condition of life in all cases studied"; and Smith, Dustman and Shull (1931) state that a saturation deficit "must always exist in growing plants."

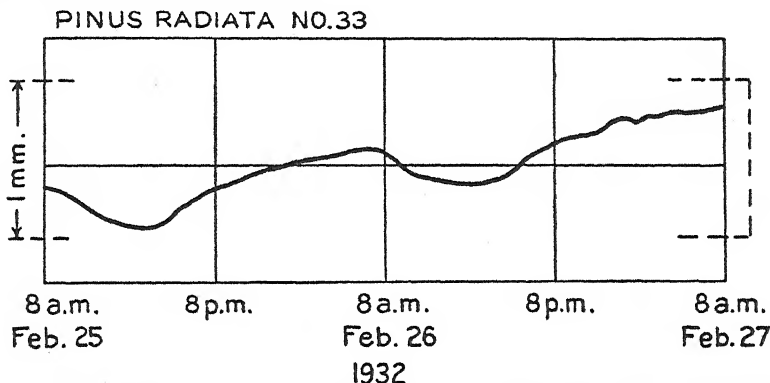


Fig. 28—Dendrographic record for Monterey pine tree showing diurnal fluctuations during period of diametral increase.

At any rate, it is evident that during the day certain tissues of the tree become appreciably depleted of water. Furthermore, as has been shown, the greatest part of this loss seems to be in the immediate vicinity of the cambium. When the tension is relieved at the upper ends of the sap columns in the tree, it appears that the intake of moisture through the roots is great enough to allow the partially dried tissues to take up water, and consequently to swell.

Occasionally there occurs an obliteration of the diurnal diametral shrinkage. This may happen either in rainy weather or when a plant is irrigated. It occurs occasionally when growth is active. Aside from these cases our records have not shown that when the transpiration rate is high, water can enter the roots of a plant fast enough to prevent diurnal shrinkage.

While the method whereby food substances are carried down the stem is an unsettled question, MacDougal has surmised that in Monterey pine the outermost layer of wood may possibly serve as a path for the downward conduction of carbohydrates (1925,¹ 26, 27, 29-30, 89; 1926,¹ 6). From

experiments of MacDougal, Overton and Smith (1929, 65, fig. 20) with dyes localized in particular annual layers of willow stems, it appears that liquids may travel downward in the outer growth layers of those trees also. This action the authors consider as probably due to "a negative force in the cohesive water-columns in the vessels."

It seems possible that when the hydrostatic tension is reduced at night and the tissues begin to fill with water derived from the soil, conditions in woody plants may favor access of moisture to the outermost layer of xylem and external tissues from above rather than from below. This would promote the movement of elaborated foods from the leaves down the stem. It would also favor nocturnal rather than diurnal growth. This, however, is still to be demonstrated. That it is true for all plants seems doubtful from the experiments of Harvey (1922²) wherein individuals of many herbaceous species were grown to maturity in continuous light. He states specifically: "It seems unnecessary to have a period of darkness to allow translocation of the assimilate from the leaves."

SEASONAL SHRINKAGE

The long-period shrinkage occurring in a dry warm season is evidently due to the inability of the plant to make up at night for the successive diurnal water losses. The amount of shrinkage occurring during the bright

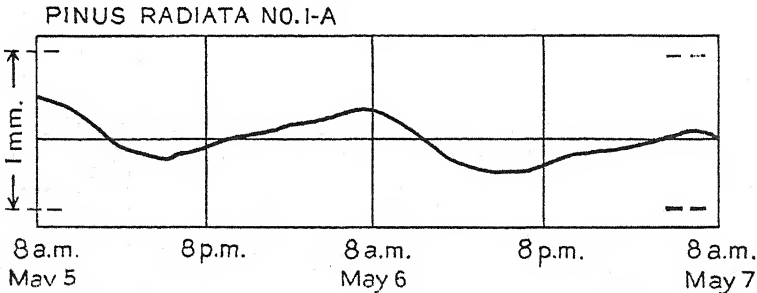


FIG. 29—Dendrographic record for Monterey pine tree showing diurnal fluctuations during period of diametral decrease.

part of the day is determined primarily by the evaporating power of the air. If, then, the plant is for any reason unable to compensate for this loss during the ensuing period of darkness, the diameter will be less at the end of the second night than at the end of the first (fig. 29). Desiccation of the soil below a certain point (varying with the character of the soil) would of course make it impossible for the plant to receive any additional moisture through its roots. It might even lose water to the soil (Magistad and Breazeale, 1929). The seasonal shrinkage, in other words, is due to a state of increased hydrostatic tension in the conducting elements, prolonged over an extended period of time.

The time of year at which dry-season shrinkage occurs is exceedingly variable. The dendrographic records show that it has begun at Carmel as

early as the end of March in an unusually dry year. On the other hand, it may in some years entirely fail to take place.

In figure 21 the diametral changes, week by week, are shown graphically for Monterey pine No. 1 from the spring of 1920 to the spring of 1933. For each season there are two graphs, one of the changes occurring at a height of 1 meter from the ground, the other at 8 meters.

It will be noted from this figure that even in the autumn following irrigation slight shrinkages may occur. Presumably if the tree had not been irrigated in the summer of 1920, contraction would have begun earlier and would have developed into a typical seasonal shrinkage. The July irrigation in 1924 appears to have been insufficient to prevent autumnal shrinkage at the upper instrument, although no shrinkage of a seasonal nature occurred at the lower point of study. It seems certain that an additional irrigation, in mid-September 1920, for example, or in August 1924, would have prevented the contractions which occurred. The graphs, then, would have been somewhat like those of 1921-22 and 1922-23.

The differences in pattern of diametral changes from year to year, which are shown in figure 21, are determined by so great a complex of factors that it would be a matter of extraordinary difficulty to analyze them with any assurance of accuracy. Fundamentally, of course, they are dependent primarily upon the amount of moisture in the soil and the evaporativity of the environment, the latter of which is the resultant of air moisture, air temperature and air movement, and the drying effect of solar radiation. It does not seem profitable at the present time to try to correlate the observed changes with the details of environmental conditions. Nor will any attempt be made here to explain the several minor differences between the two graphs for a given season.

It has been suggested by Priestley (1930) that as the water content of the wood in a dicotyledonous tree becomes reduced by high transpiration rates, water in the rays is gradually displaced by air, and that, when this happens in the cambial region, growth ceases; that, on the other hand, when the air in the cambial region is again replaced by water (in the spring), growth is resumed; and that the same conditions are effective, to a lesser extent, in conifers.

The reduction in amount of daily fluctuation which occurs with the continuance of desiccating conditions is not to be considered to be due to a decreased hydrostatic tension as drouth progresses. Rather is it to be laid to the fact that insufficient water enters the plant at night to relieve the tension as it is regularly relieved nocturnally when the soil moisture supply is adequate. If the length of the night could be increased, perhaps the story would be different.

In figure 30 is presented a comparison of the diurnal fluctuations of two Monterey pine trees for the same week in autumn. These trees stand 12 dkm. apart, but one (No. 33) is situated 11 meters lower than the other. The location of the lower tree is such that it is much better supplied with moisture than the upper. This difference was especially well marked at the time indicated, which had been preceded by an exceptionally long

dry period. The graphs of this figure indicate quite clearly that diurnal fluctuations are to a high degree dependent upon soil moisture.

This concept is further borne out by the sustained amplitude of diurnal fluctuation in healthy trees with a plentiful water supply. Figure 31 gives examples of diurnal fluctuations in a tree which had its roots actually under water, an extreme case. This is a record for the tree in a practically leafless state and for that reason the amplitude would not be very large, even with a smaller amount of soil moisture (see fig. 4). The significant fact illustrated is that diurnal shrinkages occurred even though there was no question about the abundance of moisture in the soil. The weather during this week was prevalently clear.

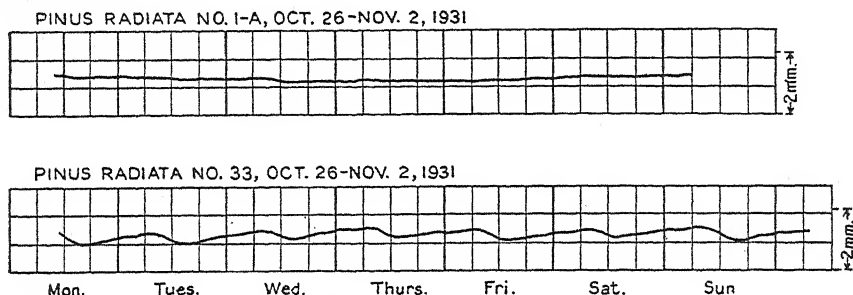


FIG. 30—Dendrographic records of two Monterey pines for same week, showing difference in amplitude of diurnal fluctuations correlated with difference in soil moisture content. Tree No. 33 was situated 11 meters lower than other and was much better supplied with water at time of year indicated. Record of No. 1-A is incomplete because of clock stoppage.

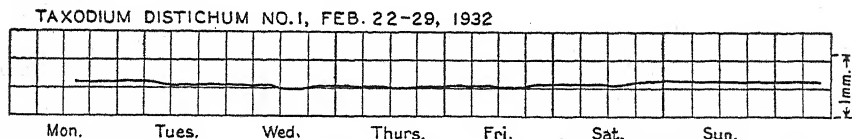


FIG. 31—Dendrogram of bald cypress showing diurnal fluctuation with plentiful water supply. At time record was made roots of tree were under water. Small amplitude of fluctuation is attributable to fact that tree was in practically leafless condition.

An effort was made to ascertain the amount of moisture in different regions of Monterey pine tree trunks at several times of year. The results of the study as conducted, however, are not very conclusive. For this investigation, cores about 15 to 25 cm. long were extracted from the trees at a height of one or two meters, by means of the Swedish increment borer. These cores were divided into inner and outer sections, the former appearing dry by ocular inspection, the latter moister. The length of the moister portion varied considerably both with the season and between trees; and no division could be made into heart- and sap-wood. In one or two instances both ends of the section appeared moist, and the core was simply broken in two arbitrarily. Samples were taken in October after a period of dry weather in which the pine trees had experienced considerable seasonal shrinkage; at the end of December after the heaviest monthly rainfall of record at Carmel (in 23 years); and near the end of February,

at which time the rainy season had lasted nearly 4 months (fig. 9). After weighing, the blocks were oven-dried at about 100° C. to constant weight and the original moisture content computed as a percentage of the dry weight of the wood. All trees studied were near the top of the fixed dune at the Coastal Laboratory. Moisture contents ascertained in this study are presented in table 16.

TABLE 16—*Moisture content, in percentage on basis of dry weight of wood, in several trees of Monterey pine.*

Diameter of tree at sample point	Tree No.	Height of sample point	Side of sample point ¹	Section of sample	Date of sampling		
					Oct. 1931	Dec. 1931	Feb. 1932
cm.		m.					
28	..	1	C	Inner	55	93	100
			N & S	Outer	118	108	92
54	1	2	N	Inner	34	90m	30
			N	Outer	114	92	91
84	28	2	S	Inner	31	28	35
			S	Outer	93	84	84
75	..	1	N	Inner	32	81m	39
			N	Outer	29	85	84
71	..	1	N	Inner	31	32	32
			N	Outer	88	78	72

¹ C=middle of tree, N=north side, S=south side,
m=inner section was apparently moist rather than dry.

From the figures of table 16 it appears that in all the samples examined there was just beneath the cambium a layer of wood in which the moisture content was relatively high. The thickness of this layer varied from 5 to 17 cm. and included from 8 to 32 growth layers. In the larger trees, furthermore, there was an appreciably drier part within the outer, moister portion.

In neither of these regions did there appear to be a marked difference in moisture content clearly referable to the soil moisture conditions. If anything, the moisture content in the outer (moister) wood appeared to be greater when the soil moisture was deficient than after soaking rains had occurred. This would indicate that the shrinkages shown by the dendrographic studies are not located principally in these moister regions of about 25 growth layers. To two of these trees (Nos. 1 and 28) dendrographs were attached, and the records show that at the time the first samples were taken on October 15 the trees had been decreasing in diameter for some months past (fig. 9).

In several samples the moisture content of the inner wood is seen to be around 30 to 35 per cent. This is very close to the moisture content in wood of various kinds in the state which has been called the "fiber-saturation point." In this condition the cell walls are saturated but the cell cavity is free of water. Observations by Stamm (1929) indicate that the fiber-saturation point at 24° to 27° C. was about 30 per cent for wood of various species. His observations for ponderosa pine show a range of from 28.5 to 31.5 per cent. It is at the fiber-saturation point that a drying fiber begins to shrink.

The amount of moisture in the bark and wood of several species of oak has also been the subject of some investigation, and the results of these studies are here presented in table 17.

TABLE 17—Moisture content of oak (*Quercus*) stems.¹

Species	Sample No.	Date of sampling	Description of sample	Wood	Bark	Wood and bark	Avg.	
agrifolia	18	1930		75		
	19	Oct. 21	From living plant.	75	90	78	77	
	20			78		
	23	22	From middle of submerged portion. ²	88		
	28	22	From just above submerged portion. ²	69	100	77	82	
	29			87		
	34	22	From leafy portion of branch ²	81	81	
	35			81		
	hypoleuca	1	Sept. 4	From living plant (Stem No. 2-A cut Sept. 3).	74	73	74	72
		2			72	63	68	
3		75		
4		27			From excised stem No. 2-A after standing in water 24 da.; sections from above water-level.	57	53	
5			54	37		49		
6				52		
7			27	From submerged portion of excised stem No. 2-A.		63	59	62
8		Oct. 7	From upper part of excised stem No. 2-A after standing in water 10 da. more; sections from above water level.	68	73	69	70	
9				70		
10				75	64	71		
11		7	From submerged portion of excised stem No. 2-A.	67	70	68		
15		21	From living plant.	89	93	
16				76	150	90		
17				100		
22		22	From middle of submerged portion. ²	106		
26		22	From just above submerged portion. ²	113	150	120	109	
27				97		
32		22	From leafy portion of branch ²	111	106	
33				100		
reticulata	12	Oct. 21	From living plant.	79	81	
	13			69	120	81		
	14			83		
	21	22	From middle of submerged portion. ²	83		
	24	22	From just above submerged portion. ²	82	113	90	89	
	25			88		
	30	22	From leafy portion of branch ²	89	89	
	31			89		

¹ Percentages are based on dry weight.² From branch cut Oct. 21, after standing 1 day in water.

During the summer and fall of 1930 studies were made of diametral changes in excised branches of whiteleaf oak. One such branch (No. 2-A) was cut off the tree on September 3, a portion removed from the bottom, and the butt of the leafy top stepped in a reservoir of tap water. The submerged butt of this branch was 21 mm. in diameter, the wood 18 mm. Sections cut the following day from the middle of the discarded portion were found to have an average moisture content of 72 per cent. After the branch had remained in water 24 days, the lower end was sawed off and the new butt replaced in the reservoir. Samples taken from the middle of the lower end (and above the level at which water had stood) had a moisture content of 52 per cent. Even a piece from below the water-level contained only 62 per cent. In other words, the samples taken from the stem just after its connection with the soil was discontinued showed a considerably higher moisture content than the samples from the stem which had had the butt end in water for over three weeks. This is especially noteworthy because of the fact that when the cut stem was placed in water it immediately swelled to a very appreciable extent, as indicated by the auxographic record. The increase in 5 days amounted to 0.14 mm. or 0.009 of the diameter under measurement. After this the stem shrunk again, 0.28 mm. (0.019 of the diameter) in 19 days. Removal of an additional section from the lower end was then followed by renewed swelling, amounting to 0.28 mm. in two days. This increase, it will be noted, just balanced the decrease of the immediately preceding days.

On August 25, a few days before the excision of this stem, the soil moisture content (based on the dry weight of the soil) had fallen to the following values: at 3 cm., 3 per cent; at 15 cm., 4 per cent; at 30 cm., 6 per cent. For several weeks prior to the removal of the stem (2-A) from the plant, it had been suffering considerable shrinkage in diameter. This of course would be expected in view of the small amount of soil moisture.

In another study, later in the season, it was found that cut stems of three species of oak, whiteleaf, netleaf (*Quercus reticulata*), and coast live, stepped in water reservoirs, all took up an appreciable amount of water in the course of a 1-day period (table 17). While the soil moisture content in the vicinity of these trees was not ascertained at this time, observations on samples taken 2 dkm. distant in both August and October indicate that the soil near the oak trees studied was appreciably drier at the end of September than two months previously.

From these observations it seems evident that the cut twigs of whiteleaf oak, whose bases were kept in water for periods of several weeks, experienced a plugging of the conducting vessels. It is not known whether this was caused by algal or bacterial growth, by deposition of suspended materials from the tap water used or by changes in materials occurring within the stem itself. With the conducting vessels plugged and transpiration continuing, shrinkage of the stem would be inevitable. At the time the experimentation with branch No. 2-A was discontinued, in early October, it still carried about 8/10ths of the green leaf area that it had had before the severance from the stem was performed.

It will be observed that in none of these studies of oak stems was the wood found to have reached a stage of dryness anywhere near the fiber-saturation point as reported by Stamm (1929).

TRAUMATIC AND PROLONGED SHRINKAGE

The prolonged cessation of wood production or actual shrinkage in diameter which has been observed near the base of an evergreen tree under certain conditions (as expounded in the section on Traumatic and Prolonged Shrinkage) is probably to be explained in a somewhat different way. In these cases we have to take into consideration a total leaf area which is relatively small for the tree. In the wind-dwarfed tree the reduction of leaf area is caused by constant dying back of the branchlets; in the other trees observed, by deliberate traumatism of various kinds. The net result is much the same: the food-producing factory is inadequate to meet all the building needs of the tree, and hence some parts of the tree do not receive a supply of these materials, with the result that growth fails to occur and sometimes shrinkage takes place.

There is indication, both in Monterey pine and in redwood, that the food substances elaborated by photosynthetic activity in the leaves are used first nearest the point of production. If there are any more of these materials, they are then used lower down in the tree. If not, growth in the lower part of the tree fails to take place. In the wind-dwarfed tree, new leaves and branchlets were formed, and perhaps new wood on the upper bole, but significant increase in diameter of the lower bole apparently did not occur. In the decapitated redwood, the branches grew while the bole, for the most part, did not. In defoliated evergreen conifers the building is of leaves and new shoots, and the diameter of the main stem near the ground does not increase at all, or only at a reduced rate. And so on. The abnormally small leaf surface could well be regarded as responsible for such inadequate supplies of building materials.

Probably somewhat similar relations are existent in the case of most deciduous trees in the spring. Here, too, there appears to be a decided tendency for the elaborated food to be first used for building near the point of production, only later becoming available in more distant parts of the tree. It is not surprising that when the naturally evergreen Monterey pine or redwood has its leaf surface reduced to a condition approximating that of a deciduous tree, the relations between leaf development and stem enlargement tend to parallel those obtaining in a deciduous tree. It may indeed be that the growing leaves in both deciduous trees and defoliated evergreen conifers draw upon the building materials manufactured in some of the older leaves, and that the needs of these must be satisfied before appreciable diametral increment can be expected.

Priestley (1930) states that "the axis of the tree, when cambial activity commences, is covered with little wedges of new tissue . . . formed from the separate renewal of activity beneath each bud," and refers to Hartig (1862) and Simon (1914) as earlier observers of this phenomenon (p. 324). If, now, insufficient food were elaborated for the extension of these wedges along and around the stem during any growing season, parts of the bole

would obviously fail to experience radial growth that season. Examination of the stem of redwood No. 9, eight years after it had been decapitated, shows that such occurrences actually took place in this tree. At the bases of new branches, the successive annual layers of new growth extended on the bole progressively farther from the branch axis, although on the whole bole accretion was slight. It seems certain that with the enlargement of the branches, the seasonal production of building materials would have been sufficient for adding new tissues to the bole throughout its length (*cf.* Haasis, 1932,⁷ 1933⁴). This concept may explain the observation of Nördlinger (1871) that in most trees winter removal of the branches was followed by suspension of radial growth during the ensuing vegetative season, and the opinion of Jost (1893) that "a distal connection with some growing leaf-structures or buds is necessary for the occurrence of radial growth," which are quoted by Grossenbacher (1915, 9).

For those cases in which diametral increase in deciduous trees has been reported to take place before the leaves have reached or approached full size, there are two or three possible explanations. The increase may be dependent upon the presence of stored food reserves which can be utilized for this purpose. It may be that building materials elaborated in the leaves become available to the bole as soon as the slightest exposure is made of green leaf surface. Or in some species, green tissues in the bark may permit of photosynthetic activity before the leaves are functioning to their full extent. In cases where records of enlargement are based upon external measurements, as in dendrographic studies, rather than upon observations of cell multiplication, the observed increase may perhaps be due to rehydration of previously dried tissues.

According to the results of studies by Hastings (1900), growth can be expected to begin on the older twigs first in northern white pine and in a species of hemlock which holds its leaves for six or seven years, whereas in the deciduous bald cypress this investigator observed that the younger branches started growing before the older ones. These observations indicate that diametral growth in trees begins in the spring in the vicinity of the greatest number of leaves. When a tree has a full complement of leaves of several ages at the beginning of the season, growth begins on the older twigs. When some of the leaves have been removed, naturally or artificially, growth begins on the younger parts. In the case of a Monterey pine tree (No. 1) to which two dendrographs were attached 7 meters apart, the time of beginning of growth was much the same year by year at the two heights (fig. 21).

Why sustained shrinkage should occur in the lower bole of some of the trees whose leaf area is inadequate for normal development is not entirely clear. Perhaps it is to be explained by some such train of events as the following: The lack of plentiful food supplies in the sap stream results in a deficient amount being available for the roots; the roots fail to extend into new soil masses; the available moisture in the soil adjacent to the roots has been removed by the roots; with a reduction or lack of additional accretions to the roots, water for photosynthesis is drawn from the body of the plant; and we have the anomalous condition of a net shrinkage in bole

diameter traceable to a reduced leaf surface. As we have seen, the lessened amount of transpiration due to reduced leaf area may, at other times, apparently be responsible for lack of diurnal shrinkage.

A reduction of root development may also be an aggravating cause of the seasonal or long period types of shrinkage. It is conceivable that after the soil moisture content has reached a certain low point, the amount of food produced in the leaves might well be limited by the amount of water available in the leaves over and above that transpired. If, then, with this limitation of building materials, a smaller proportion of these were available for accretions to the roots, these would make relatively slow additional growth. Probably they would eventually cease to grow at all, perhaps even before top growth came to a standstill. Accepting the principle that roots in a dry soil can not depend upon the moisture traveling to them through the soil, but must be continually growing into fresh soil masses if they are to exhaust the soil moisture with any degree of thoroughness (*cf.* Livingston, 1927,¹ 1927;² Veihmeyer, 1927, 231-235; Wilson, 1927), it is obvious that any retardation of root growth would have as a prompt sequel a further reduction of the amount of root water entering the transpiration stream. This latter of course would result in there being yet less building material available to the roots.

It seems likely that the prolonged shrinkage of palo verde may be attributable in part to reduced root growth brought about by desiccation of the soil. It is probable also that diametral shrinkage may to some extent be incident to the withdrawal of stored food substances used in branch elongation (*cf.* Pfeffer, 1903, 13). The removal of water from one part of the plant to another may also be held partly accountable for such shrinkage. The subject of withdrawal of water from fruits by leaves has been discussed in a number of papers (*cf.* Bartholomew, 1926); and Moinat (1932), on the basis of studies with beans (*Phaseolus vulgaris*) surmised that just prior to permanent wilting the plants were using for transpiration stored water from their own tissues more than from the soil.

Evidently, if any large number of the water strands in the tree become broken, death of the top of the tree, or of the entire tree, may readily ensue. Occurrences of this sort have been observed in times of drouth of unusual severity for the region concerned (*cf.* Hursh and Haasis, 1931). The more frequent incidence of such periods of drouth might of course easily result in the exclusion or elimination of a tree species from a locality. If, for instance, a dry period like that occurring in the spring, summer and fall of 1931 (fig. 9) were followed on the Monterey Peninsula by a relatively dry winter and then a number of similarly dry years, it is entirely probable that many of the Monterey pines would perish. A change in wind direction or intensity, persisting over a period of years, might well push back the redwood timber line in the coastal canyons of Monterey County. While we have instances of prolonged shrinkage for many years of individual trees of divers species, the race obviously could not survive if climatic conditions favoring the process continued indefinitely.

OTHER CAUSES OF FLUCTUATION

Diametral changes reported by other observers which appeared to be correlated with other factors than those just dealt with may be dismissed briefly. Brown (1915) ascribed a winter phloem contraction in white pine to extremely low temperatures. Since extremely cold weather is not experienced in the Carmel region, this of course can not be the cause of the seasonal shrinkages discussed in the present paper. It has already been suggested how this might have been an indirect effect. Hall (1891) made the observation in Uruguay that a decrease in diameter in eight trees of four deciduous species was apparently synchronous with the autumnal leaf fall. Such a decrease was not shown by eight evergreen trees including one species of pine. In this case, neither dry soil nor cold weather can be looked upon as causing the shrinkage, since the mean temperatures for April and May (when the leaf fall largely occurred) were not the lowest for the year and the amounts of rainfall were somewhat above the monthly average.

TABLE 18—List of individual trees and other plants used in dendrographic and ausographic studies and referred to in the text.*

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Ash, velvet (=Ash, Arizona)	Fraxinus velutina Torr. (=Fraxinus arizonica)	..	3 dm	Tucson, Ariz.	32° N.	700	Residence grounds	1919-21		MacDougal, 1921; ¹ OR
Ash, white	Fraxinus americana L.	Syracuse, N. Y.	43° N.	...				Lodewick, 1925
Ash, white	Fraxinus americana L.	1	5 cm	4 m	Carmel, Calif.	*	*	Moist (lower garden)	1933	Pedigreed tree with ascidial leaves from Dr. G. H. Shull (No. 10456 (4))	OR
Bagote Bald cypress	See <i>Horsebean</i> <i>Taxodium distichum</i> Rich.	.. 1 1 cm 1 m	Carmel, Calif. *	...	Moist (lower garden)	1932-33	Planted	OR
Beech, (American)	<i>Fagus grandifolia</i> Ehrh.	Baltimore, Md.	39° N.	...		1919		MacDougal, 1921; ¹ OR
Boxelder	<i>Acer negundo</i> L.	Ogden, Utah	41° N.	...		1920		Korstian, 1921
Bunya-bunya	<i>Araucaria bidwillii</i> Hook.	1	3 cm	1 m	Carmel, Calif.	*	*		1932-33	In can set in ground	OR
Cactus, giant	<i>Carnegiea gigantea</i> Britt. (=Cereus giganteus Engelm.)	33	2 m ^a	Tucson, Ariz.	32° N.	700		1924-32		OR
California laurel (=California bay)	<i>Umbellularia californica</i> Nutt.	1	2 dm	10 m	Rocky Creek Canyon	*	*	N. exposure	1931-32		OR

Cottonwood, eastern	<i>Populus deltoides</i> Marsh. (= <i>Populus deltoides</i>)	..	4 dm	St. Louis, Mo.	39° N.	1919-20	MacDougal, 1921, ¹ 1924, ¹ OR
Cottonwood, MacDougal	<i>Populus macdougalii</i> Rose	..	2 dm	Continental, Ariz.	Near irrigation ditch	1920	MacDougal, 1921, ¹ 1924, ¹
Cottonwood, MacDougal	<i>Populus macdougalii</i> Rose	..	4 dm	Tucson, Ariz.	32° N.	700	Residence grounds	1921	MacDougal, 1924, ¹ OR
Cypress, Monterey	<i>Cupressus macrocarpa</i> Gord.	2	2 dm	Carmel Highlands, Colo.	*	*	Residence grounds	1931-33	Planted
Douglas fir	<i>Pseudotsuga taxifolia</i> Britt.	..	4 dm	Pikes Peak, Colo.	39° N.	...	S. E. exposure	1920	MacDougal, 1921, ¹ OR
Dracena	<i>Cordylone australis</i> Hook.f.? (= <i>Dracaena australis</i> Forst.?)	..	6 cm	1 m	Carmel, Calif.	*	*	Dry (part of time in box; part of time planted on dune)	1930-31	OR
Elm, American	<i>Ulmus americana</i> L.	New York, N. Y.	41° N.	1931	OR
Hard pear	<i>Olinia cymosa</i> Thunb.	12 m	Deepwells, Knysna, S. Afr.	34° S.	Phillips, 1931
Horsebean	<i>Parkinsonia aculeata</i> L.	..	2 dm	Tucson, Ariz.	32° N.	700	Residence grounds	1921	MacDougal, 1924, ¹ OR
Horsebean, little-leaf	<i>Parkinsonia microphylla</i> Torr.	..	1 dm	Tucson, Ariz.	32° N.	700	Laboratory grounds	1920	MacDougal, 1924, ¹ OR
Horsebean, little-leaf	<i>Parkinsonia microphylla</i> Torr.	..	1 dm	Tucson, Ariz.	32° N.	700	1929-33	OR
Laurel, California	See <i>Californica laurel</i>

* For the most part the dendrographic contacts on plants 5 cm. or more in diameter were at a height of about 1 meter above the ground. Carmel, Carmel Highlands, Palo Colorado Canyon and Rocky Creek Canyon are localities in Monterey County, California, at 36° N. Lat. (cf. Introduction); the Carmel sites are described in the Introduction; the trees studied were situated at the following elevations above sea-level, Carmel 20 to 40 meters (100 ft.), Carmel Highlands about 150 meters (500 ft.), Rocky Creek 100 to 200 meters (300 to 600 ft.). In cases where instruments were in operation on a tree for a period of several years, recent measurements are dated as follows: a = 1931, b = 1932, c = 1933; dates of other measurements are indicated by under "Notes" or "Sources of Information." OR = original records (including verbal information supplied by Dr. D. T. MacDougal and observations by the writer, as well as dendrographic records and accompanying notes). With the possible exception of bunya-bunya, all the plants listed in this table showed diurnal fluctuations at one time or another. The nomenclature in the main follows that given by Sudworth (1927).

TABLE 18—List of individual trees and other plants used in dendrographic and auxographic studies and referred to in the text.*—Cont.

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Maple, ash-leaved	<i>See Boxelder</i>	1	2 dm	13 m	Rocky Creek Canyon	OR
Maple, bigleaf	<i>Acer macrophyllum</i>	1	2 dm	...	New York, N. Y.	41° N.	*	N. exposure	1931-32	...	OR
Maple, Sugar	<i>Acer saccharum</i>	1	1 cm	...	Carmel, Calif.	*	*	Greenhouse	1920	In box	OR
Maize	<i>Zea mays</i> L.	1	1 cm	...	Carmel, Calif.	...	*	...	1919-20	...	MacDougal, 1916,* 1921*
Nogal	<i>See Walnut, Arizona</i>	1	4 dm	...	Carmel, Calif.	*	*	Dry (dune)	1920	...	MacDougal, 1921*
Oak, coast live	<i>Quercus agrifolia</i> Née	2	2 dm	...	Carmel, Calif.	*	*	Dry (dune)	1931-33	From same root as No. 2. Instrument No. 3 (1931-3), contacts on intact bark, 21 cm. between contacts; No. 3-B (1933), contacts on recent wood, 16 cm. between contacts; No. 3-A (1931-3), contacts on older wood, 9 cm. between contacts.	OR
Oak, coast live	<i>Quercus agrifolia</i> Née	3	2 dm	8 m	Carmel, Calif.	*	*	Dry (dune)			

ak, coast live ak, whiteleaf	Quercus agrifolia Née Quercus hypoleuca Engelm.	4 2	3 dm 5 cm	7 m 4 m	Carmel, Calif. Carmel, Calif.	* *	* *	Dry (dune) Moist (lower garden)	1933 1930-31 Raised from Ariz. seed; dendrographic study of trunk (2); auxo- graphic study of branch (2-A) 15 mm. in diam.	OR OR
range, sweet	Citrus sinensis Engl.	Riverside, Calif.	34° N.	1920	Dr. H. S. Reed (letter); MacDougal, 1921; ¹ OR
regon myrtle alo verde	See California laurel See Horsebean, little-leaf
ine, Arizona	Pinus arizonica Engelm. (= Pinus ponde- rosa arizonica Shaw)	1	2 dm	Near Tucson, Ariz.	32° N.	2400	N. exposure	1922	MacDougal, 1924 ¹
ine, Arizona	Pinus arizonica Engelm. (= Pinus ponde- rosa arizonica Shaw)	2	Near Tucson, Ariz.	32° N.	2400	S. exposure	1922	MacDougal, 1924 ¹
ine, Chihuahua	Pinus leiophylla Schlect. and Cham. (= Pinus chihua- huana Engelm.)	..	4 dm	Near Tucson, Ariz.	32° N.	2000	1919	MacDougal, 1921 ¹
ine, Mexican white	Pinus strobi- formis Engelm.	..	4 dm	Near Tucson, Ariz.	32° N.	2400	1922	MacDougal, 1924 ¹

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Pine, Monterey	<i>Pinus radiata</i> D. Don	1	6 dm ^b	26 m ^c	Carmel, Calif.	*	meters *	Dry (dune)	1918-33	1920: height 25 m., diam. 4 dm. Instrument No. 1A (1918-33) at height of 1 m., (diam. 6 dm. ^b). Instrument No. 1-B (1920-33) at height of 8 m. (diam. 5 dm. ^b); No. 1-C (1923-9, 1932-3) on root (diam. 9 cm. ^c)	MacDougal, 1921; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	6	4 dm ^b	15 m ^a	Carmel, Calif.	*	*	Dry (dune) N. exposure	1920, 1922-33	1920: height 10 m., diam. 2 dm. Instrument No. 6 (1920, 1922-33) at height of 1 m., contacts on thinned bark; No. 6-A (1931) at height of 2 m., contacts on intact bark.	OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	10	1 dm	Carmel, Calif.	*	*	Dry (dune) N. exposure	1921-24	1922: height after decapitation, 3 m.	MacDougal, 1924; ¹ OR

ine, Monterey	Pinus radiata D. Don	14	2 dm	10 m	Carmel, Calif.	*	*	Dry (dune) N. exposure	1922-23	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	15	1 dm	Carmel, Calif.	*	*	Dry (dune) N. exposure	1922	1922: height af- ter decapita- tion, 2 m.	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	16	2 dm	Carmel, Calif.	*	*	Moist (lower garden)	1922-30	1922: 5-6 m.; 1923: height after decapi- tation, 2 m.	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	17	5 dm ^b	20 m ^b	Carmel, Calif.	*	*	Moist (lower garden)	1922-32	1922: height 5- 6 m., diam. 2 dm.	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	18	1 dm	Carmel, Calif.	*	*	Moist (lower garden)	1922-26	1923: height be- fore decapita- tion, 5-6 m.; after decapi- tation, 2 m.	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	19	1 dm	4 m	Carmel, Calif.	*	*	Dry (dune) N. exposure	1922-31	MacDougal, 1924; ¹ OR
ine, Monterey	Pinus radiata D. Don	20	3 dm	15 m ^b	Carmel, Calif.	*	*	Dry (dune)	1922-32	1923: height 6 m., diam. 1 dm. Instru- ment No. 20 (1922-32) at height of 1 m., contacts on thinned bark, 23 cm. ^a be- tween con- tacts; No. 20-B (1931- 2) at height of 1 m., con- tacts on older wood, 12 cm. ^a between con- tacts; No. 20- C (1931-2) at height of 2 m.; contacts on recent wood, 20 cm. ^a between con- tacts.	MacDougal, 1924; ¹ OR

TABLE 18—List of individual trees and other plants used in dendrographic and auxographic studies and referred to in the text.*—Cont.

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Pine, Monterey	<i>Pinus radiata</i> D. Don	21	1 dm	6 m	Carmel, Calif.	*	meters	1922-23	MacDougal, 1924; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	23	1 dm	7 m	Carmel, Calif.	*	*	Dry (dune)	1923-30	MacDougal, 1924; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	25	5 cm	4 m	Carmel, Calif.	*	*	N. exposure	1923-24	MacDougal, 1924; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	27	Carmel, Calif.	*	*	1923-25	MacDougal, 1925; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	28	8 dm ^b	22 m ^a	Carmel, Calif.	*	*	Dry (dune)	1923-33	OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	29	2 dm ^a	Carmel, Calif.	*	*	Dry (dune), N. exposure	1924-31	1924: height 4 m.; diam. 1 dm. 1925; ¹ OR	MacDougal, 1925; ¹ OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	31	2 cm ^c	2 m ^c	Carmel, Calif.	*	*	Dry (dune)	1928-33	1928: height 1 m.	OR
Pine, Monterey	<i>Pinus radiata</i> D. Don	33	2 dm ^b	9 m ^a	Carmel, Calif.	*	*	Moist (lower garden)	1930-33	OR
Pine, ponderosa (see also <i>Pine</i> , rock)	<i>Pinus ponderosa</i> Laws.	..	4 dm	Pikes Peak, Colo.	39° N.	...	S. E. exposure	1920	MacDougal, 1921; ¹ OR
Pine, rock (see also <i>Pine</i> , ponderosa)	<i>Pinus ponderosa</i> scopulorum Engelm.	..	5 dm	Near Flagstaff, Ariz.	35° N.	2200	1920	MacDougal, 1921; ¹ OR
Pine, rock (see also <i>Pine</i> , ponderosa)	<i>Pinus ponderosa</i> scopulorum Engelm.	1	4 dm	Near Flagstaff, Ariz.	35° N.	2200	S. E. exposure	1923	Pearson, 1924
Pine, rock (see also <i>Pine</i> , ponderosa)	<i>Pinus ponderosa</i> scopulorum Engelm.	2	1 dm	Near Flagstaff, Ariz.	35° N.	2200	Level	1923	Pearson, 1924

Pine, western white	<i>Pinus monticola</i> D. Don	..	3 dm	Priest River, Idaho	48° N.	1930-31	Dominant tree.	OR (Through courtesy of Mr. James C. Even- den and officers of the North- ern Rocky Mountain For- est & Range Experiment Station).
Pine, western yellow	<i>See Pine, ponderosa</i>
Poplar, Carolina	<i>See Cottonwood,</i> <i>eastern</i>
Poplar, MacDougal	<i>See Cottonwood,</i> <i>MacDougal</i>
Redwood	<i>Sequoia sempervirens</i> Endl.	2	1 dm	Palo Colorado Canyon	*	...	S. exposure	1922	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	6	5 dm ^b	Rocky Creek Canyon	*	*	N. exposure	1924-33	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	7	6 dm ^b	Rocky Creek Canyon	*	*	S. exposure	1924-33	OR

TABLE 18—List of individual trees and other plants used in dendrographic and ausographic studies and referred to in the text.*—Cont.

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Redwood	<i>Sequoia sempervirens</i> Endl.	8	2 dm ^b	Rocky Creek Canyon	*	meters *	S. exposure	1924-33	Instrument No. 8 (1924-33) at height of 1 m., contacts on thinned bark, 21 cm.* between contacts; No. 8-A (1931-2) at height of 2 m., contacts on wood 5-6 yr. old, 10 cm. between contacts.	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	9	1 dm	Rocky Creek Canyon	*	*	S. exposure	1924-32	1924: height before decapitation, 7 m.; after decapitation, 2 m.	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	10	4 dm ^a	Rocky Creek Canyon	*	*	S. exposure	1924-31	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	11	2 dm	5 m	Rocky Creek Canyon	*	100	Timber line	1924-29, 1931-32	Wind-dwarfed tree on western edge of stand.	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	13	2 dm ^c	17 m ^c	Rocky Creek Canyon	*	200	Moist	1924-30	OR

Redwood	<i>Sequoia sempervirens</i> Endl.	14	2 dm ^b	Rocky Creek Canyon	*	*	N. exposure	1924-32	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	15	2 dm	Rocky Creek Canyon	*	*	N. exposure	1924-26	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	16	2 dm ^a	Rocky Creek Canyon	*	*	N. exposure	1924, 1927-31	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	17	2 cm ^b	Rocky Creek Canyon	*	*	N. exposure	1928-32	From stump of twin of No. 14; heights 21 dm. ^a above ground, 12 dm. ^a above top of stump.	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	18	6 cm	3 m	Carmel, Calif.	*	*	Moist (lower garden)	1931	Planted.	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	19	14 dm ^b	43 m ^c	Rocky Creek Canyon	*	*	Bottom of small can- yon opening S.	1931-33	OR
Redwood	<i>Sequoia sempervirens</i> Endl.	20	3 cm	2 m	Carmel, Calif.	*	*	Moist (lower garden)	1932	Planted.	OR
Sahuaro (=Saguaro)	<i>See Cactus, giant</i>
Sapodilla	<i>Achras zapota</i> L.	British Hon- duras	17° N.	1931-32	Karling, 1932; OR
Southern cypress Spruce, blue	<i>See Bald cypress</i> <i>Picea pungens</i> Engelm. (=Picea parryana Parry)	Near Salt Lake City, Utah	41° N.	2250	Nursery grounds.	1920	Korstian, 1921
Stinkwood	<i>Ocotea bullata</i> E. Mey.	15 m	Deepwells, Knyana, So. Afr.	34° S.	Phillips, 1931
Sycamore	<i>Platanus occiden- talis</i> L.	St. Louis, Mo.	39° N.	1919-20	MacDougal, 1924; ^a OR

Common name	Scientific name	Tree No.	Diameter at contacts	Height	Locality	Lat.	Elevation above sea-level	Site	Dates of dendrographic study	Notes	Sources of information for this table
Walnut, Arizona	<i>Juglans rupestris</i> major Torr. (= <i>Juglans</i> major Heller)	1	2 dm	8 m	Carmel, Calif.	*	meters *	Moist (lower garden)	years 1920-22, 1925-31, 1933	Raised from Arizona seed from 2500 m. Instrument No. 1 with bearings on intact bark 1920-22, 1925-31, 1930, on wood Sept. 1930 - June 1931, on intact bark June - Nov. 1931, 1933 distance between contacts 23 cm. ^c No. J-4 (1933) with bearings on wood, distance between contacts 19 cm. ^c	OR
Walnut, Arizona	<i>Juglans rupestris</i> major Torr. (= <i>Juglans</i> major Heller)	2	2 dm	Near Tucson, Ariz.	32° N.	2100		1922	MacDougal, 1924; ¹ OR
Walnut, Arizona	<i>Juglans rupestris</i> major Torr. (= <i>Juglans</i> major Heller)	5	1 dm ^b	Carmel, Calif.	*	*	Moist (lower garden)	1930-33	Raised from Arizona seed from 900 m.	OR
Willow, arroyo (= Willow, white)	<i>Salix lasiolepis</i> Benth.	..	1 dm	8 m	Carmel, Calif.	*	*	Moist (lower garden)	1922	MacDougal, 1924 ¹ ; OR

SUMMARY

Observations of diametral changes other than growth in plant stems have been reported from time to time for the past half-century. Following the development of the MacDougal dendrograph in 1918, many continuous records have been made of the diametral changes in tree trunks, largely at the laboratories of the Division of Plant Biology of the Carnegie Institution of Washington.

Diurnal shrinkage and nocturnal swelling in clear weather have been found to be the rule in practically all species which have formed the subjects of dendrographic study, gymnosperms, monocotyledons and ring-porous and diffuse-porous dicotyledons. With the exception of a species of large cactus, the pattern of diurnal fluctuation is much the same for all plants studied. Weather conditions cause pronounced modifications of this pattern; any increase in the integrated evaporitvity of the environment is reflected in an increased shrinkage in tree trunks and vice versa. The maximal recorded amount of actual diurnal fluctuation for a tree of the ordinary type is 1.6 mm.; the maximal relative amount, 0.0329 of the diameter. From this maximum the amount may vary to practically none. With the continuance of dry weather the amplitude is reduced; in rainy weather the diurnal shrinkage may be obliterated; and irrigation has much the same effect. Girdling has been found to be followed by ultimate reduction of diurnal fluctuations in two tree species; decapitation was followed by immediate reduction of amplitude; defoliation of pine trees which removed most of the leaves was followed by reduction or abolition of the fluctuations. A reduced amplitude of diurnal fluctuation may be due either to a reduction of the amount of water in the tree or a reduction in the evaporitvity of the environment.

Shrinkage of trees of various species may occur during a dry summer or autumn, during the dormant season of both evergreen and coniferous trees and during the period of leaf development in the spring. When water again becomes available to the roots of a tree which has suffered dry-season shrinkage, enlargement ensues. Trees with a plentiful water supply do not experience dry-season shrinkage. Bole swelling may occur at night even though the tree is undergoing definite shrinkage from day to day. When water is available only in excessively small amounts while transpiration continues active each day, shrinkage must ensue. Seasonal shrinkage is closely related to diurnal shrinkage.

Shrinkages have been found to follow traumatism of various sorts in pine and redwood. Shrinkages of considerable duration may be caused in redwood and palo verde by the continuance for some time of unfavorable environmental conditions. The growth of some desert species must often occur in a quite interrupted manner, with alternating periods of diametral increase and decrease. The long-period shrinkage is closely related to dry-season shrinkage.

Increase in diameter of a plant stem may be due to growth or to the rehydration of previously dried tissues. The two processes may occur very close together as to time, perhaps even simultaneously. When detailed

measurements of diametral changes are begun subsequent to a period of shrinkage, any increases observed should be regarded as including rehydration effects as well as those due to actual growth. Growth is primarily dependent upon an adequate water supply and sufficient heat; both these factors may vary considerably. It appears that ordinarily cell division can take place only when the cells are turgid or nearly so; the growing tissue is not usually turgid at the time the tree bole is shrinking; and growth, therefore, is not to be expected during the daytime in clear weather. It may also be inhibited by low temperatures. There is some evidence that when moisture conditions are exceptionally favorable, growth may occur in the daytime. There is also indication that food substances elaborated by the leaves are frequently used first nearest the point of production. If there is a deficient amount of these materials at any time, growth of the lower bole may fail to take place. Cambial activity is not necessarily the same in all parts of the tree.

In the Monterey pine a very large amount of the diurnal and seasonal fluctuations in moisture content occurs in a relatively thin layer of tissues in the vicinity of the cambium; in the coast live oak most of the fluctuation occurs in the thick bark. Shrinkage and swelling are closely connected with the water balance in the tree. Any factor, such as increased air movement, which promotes transpiration favors shrinkage, while any factor retarding transpiration, such as high atmospheric humidity, favors swelling.

Depending upon differences in weather conditions, growth of native Monterey pines may begin as early as November or as late as March; and growth is often stopped by soil desiccation in the summer or fall. In Monterey County, California the growing season of redwood is approximately from April to October. Essentially continuous growth throughout the year except for diurnal shrinkage has been observed for individual trees of Monterey pine and Monterey cypress. Where the warm period of the year is also mainly dry and the moist season usually cool, evergreenness would be of great value to a plant, as with it the plant would be equipped to avail itself of every period, however short, when temperature and moisture conditions together were right for growth.

BIBLIOGRAPHY

(Asterisks (*) are prefixed to the titles of those papers in which results of dendrographic studies are presented.)

- BAILEY, I. W. 1925. The "spruce budworm" biocenose. I: Frost rings as indicators of the chronology of specific biological events. *Bot. Gaz.*, vol. 80, 93-101.
- BARTHOLOMEW, E. T. 1926. Internal decline of lemons. III: Water deficit in lemon fruits caused by excessive leaf evaporation. *Amer. Jour. Bot.*, vol. 13, 102-117.
- BROWN, H. P. 1912. Growth studies in forest trees. I: *Pinus rigida* Mill. *Bot. Gaz.*, vol. 54, 386-402.
- . 1915. Growth studies in forest trees. II: *Pinus strobus* L. *Bot. Gaz.*, vol. 59, 197-240.
- BUCKHOUT, W. A. 1907. The formation of the annual ring of wood in European larch and the pine. *Forestry Quarterly*, vol. 5, 259-267.
- BYERS, H. R. 1930. Summer sea fogs of the Central California coast. *Univ. Calif. Pubs. in Geography*, vol. 3, 291-338.
- CHALK, L. 1930. The formation of spring and summer wood in ash and Douglas fir. *Oxford Forestry Memoirs* No. 10.
- COOPER, W. S. 1922. The broad-sclerophyll vegetation of California. *Carnegie Inst. Wash. Pub.* No. 319.
- COSTER, C. 1927. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. *Ann. Jard. Bot. Buitenzorg.*, vol. 37, 49-160; 38, 1-114.
- FRIEDRICH, J. 1905. Zuwachsautograph. *Centralbl. für das ges. Forstwesen*, Bd. 31, 456-461.
- FRITZ, E., and J. L. AVERELL. 1924. Discontinuous growth rings in California redwood. *Jour. For.*, vol. 22, No. 6, 31-38.
- GROSSENBACHER, J. G. 1915. The periodicity and distribution of radial growth in trees and their relation to the development of "annual" rings. *Trans. Wis. Acad. Sciences, Arts and Letters*, vol. 18, pt. 1.
- *HAASIS, FERDINAND W. 1931.¹ A study of significance of pine bark thickness in dendrography. *Carnegie Inst. Wash. Year Book* No. 30, 243.
- *———. 1931.² Seasonal shrinkage of trees. *Carnegie Inst. Wash. Year Book* No. 30, 243-244.
- *———. 1931.³ Reversible variations in diameter of woody cylinders of trees. *Carnegie Inst. Wash. Year Book* No. 30, 244.
- . 1931.⁴ Cambial temperatures. *Carnegie Inst. Wash. Year Book* No. 30, 244-246.
- *———. 1931.⁵ Reversible variations in monocotyledonous stems. *Carnegie Inst. Wash. Year Book* No. 30, 246.
- *———. 1932.¹ Seasonal shrinkage in Monterey-pine and redwood trees. *Plant Physiology*, vol. 7, 285-295.
- *———. 1932.² Comparison of dendrographic records made by three similar instruments on one tree. *Carnegie Inst. Wash. Year Book* No. 31, 195-196.
- *———. 1932.³ Further records of essentially continuous growth in trees. *Carnegie Inst. Wash. Year Book* No. 31, 196-197.
- *———. 1932.⁴ Period of enlargement following seasonal shrinkage. *Carnegie Inst. Wash. Year Book* No. 31, 197-198.
- *———. 1932.⁵ Growth and diurnal fluctuations in a big-leaf maple and in a California laurel. *Carnegie Inst. Wash. Year Book* No. 31, 198.
- *———. 1932.⁶ Growth and diurnal fluctuations in a deciduous gymnosperm. *Carnegie Inst. Wash. Year Book* No. 31, 199.
- *———. 1932.⁷ Shrinkage in a wind-dwarfed redwood and in a decapitated redwood. *Carnegie Inst. Wash. Year Book* No. 31, 200-201.
- *———. 1933.¹ Shrinkage and expansion in woody cylinders of living trees. *Amer. Jour. Bot.*, vol. 20, 85-91.
- *———. 1933.² Shrinkage in a wind-dwarfed redwood. *Jour. For.*, vol. 31, 407-412.
- *———. 1933.³ Winter and spring shrinkages of deciduous and evergreen trees. *Carnegie Inst. Wash. Year Book* No. 32, 190-191.
- . 1933.⁴ Growth of a redwood (*Sequoia sempervirens*) subsequent to decapitation. *Carnegie Inst. Wash. Year Book* No. 32, 191-192.
- HALL, C. E. 1891. Notes on tree measurements made monthly at San Jorge, Uruguay, from January 12, 1885, to January 12, 1890. *Trans. Bot. Soc. Edinburg*, vol. 18, 456-468.
- HANSEN, H. C., and B. BRENKE. 1926. Seasonal development of growth layers in *Fraxinus campestris* and *Acer saccharinum*. *Bot. Gaz.*, vol. 82, 286-305.

- HARTIG, ROBERT. 1870. Zur Lehre vom Dickenwachsthum der Waldbäume. Botan. Zeitg., Bd. 28, 505-513, 521-529.
- HARTIG, TH. 1862. Ueber die Bewegung des Saftes in den Holzpflanzen. Botan. Zeitg., Bd. 20, 73-76, 81-87, 97-100, 105-109. (Cited by Priestley, 1930.)
- HARVEY, R. B. 1922.¹ Growth of plants in artificial light from seed to seed. Science, vol. 56, 366-367.
- . 1922.² Growth of plants in artificial light. Bot. Gaz., vol. 74, 447-451.
- . 1923. Cambial temperatures of trees in winter and their relation to sun scald. Ecology, vol. 4, 261-265.
- HASTINGS, GEO. T. 1900. When increase in thickness begins in our trees. Plant World, vol. 3, 113-116.
- HAWLEY, L. F. 1931. Wood-liquid relations. U. S. Dept. Agric. Tech. Bul. 248.
- HUNTINGTON, ELLSWORTH. 1928. The secret of the big trees. U. S. National Park Service.
- HURSH, C. R., and F. W. HAASIS. 1931. Effects of 1925 summer drought on Southern Appalachian hardwoods. Ecology, vol. 12, 380-386.
- JEPSON, W. L. 1910. Silva of California. Mem. Univ. Calif. vol. 2.
- JOST, L. 1893. Ueber Beziehungen zwischen der Blattentwicklung und der Gefassbildung in der Pflanze. Botan. Zeitg., Bd. 51, 89-138. (Cited by Grossenbacher, 1915.)
- . 1907. (Gibson, R. J. Harvey, trans.) Lectures on Plant Physiology.
- KAISER, P. 1879. Ueber die tägliche Periodicität der Dickendimensionen der Baumstämme. Inaug. Diss. Halle.
- *KARLING, J. S. 1932. Dendrograph studies on *Achras zapota* in relation to the most favorable time for tapping. Mimeographed abstract of paper presented before meeting of American Society of Plant Physiologists, Dec. 30, 1932.
- KIRKWOOD, J. E. 1914. The influence of preceding seasons on the growth of yellow pine. Torrey, vol. 14, 115-125.
- KNUDSON, L. 1913. Observations on the inception, season, and duration of cambium development in the American larch (*Larix laricina*). Bull. Torr. Bot. Club, vol. 40, 271-293.
- *KORSTIAN, C. F. 1921. Diameter growth in box elder and blue spruce. Bot. Gaz., vol. 71, 454-461.
- KRAMER, P. J. 1932. The absorption of water by root systems of plants. Amer. Jour. Bot., vol. 19, 148-164.
- KRAUS, G. 1877. Die Vertheilung und Bedeutung des Wassers bei Wachstums- und Spannungsvorgängen in der Pflanze. Botan. Zeitg., Bd. 35, 595-597.
- LIVINGSTON, B. E. 1927.¹ Plant water relations. Quart. Rev. of Biology, vol. 2, 494-515.
- . 1927.² Water relations of the plant as a whole. Carnegie Inst. Wash. Year Book No. 26, 290-295.
- , and F. W. HAASIS. 1929. The measurement of evaporation in freezing weather. Jour. Ecology, vol. 17, 315-328.
- LLOYD, F. E. 1912. The water relations of sclerophylls and similar ecological types. Carnegie Inst. Wash. Year Book No. 11, 61.
- . 1916. Growth of *Eriogonum* in relation to light, temperature, and transpiration. Carnegie Inst. Wash. Year Book No. 15, 58-59.
- *LODEWICK, J. E. 1925. Growth studies in forest trees. III: Experiments with the dendrograph on *Fraxinus americana*. Bot. Gaz., vol. 79, 311-323.
- . 1928. Seasonal activity of the cambium in some Northeastern trees. N. Y. State College Forestry Tech. Pub. 23.
- MACDOUGAL, D. T. 1903. The influence of light and darkness on growth and development. Memoirs N. Y. Bot. Gard. 2.
- . 1916.¹ Mechanism and conditions of growth. Memoirs N. Y. Bot. Gard. 6, 5-26.
- . 1916.² The distensive forces in growth. Carnegie Inst. Wash. Year Book No. 15, 59-61.
- . 1918.¹ The nature and course of growth in higher plants. Carnegie Inst. Wash. Year Book No. 17, 58-59.
- . 1918.² The dendrograph; a new instrument for recording growth and other variations in the dimensions of trees. Carnegie Inst. Wash. Year Book No. 17, 59-60.
- *———. 1919.¹ Growth in organisms. Science n.s., vol. 49, 599-605.
- . 1919.² The dendrograph. Carnegie Inst. Wash. Year Book No. 18, 72-74.
- *———. 1919.³ Growth of the Arizona ash. Carnegie Inst. Wash. Year Book No. 18, 74-75.
- *———. 1919.⁴ Growth of the Chihuahua pine. Carnegie Inst. Wash. Year Book No. 18, 75.

- *MACDOUGAL, D. T. 1919.⁵ The growth of the Monterey pine. Carnegie Inst. Wash. Year Book No. 18, 75-77.
- *———. 1919.⁶ The growth of an oak trunk. Carnegie Inst. Wash. Year Book No. 18, 77.
- *———. 1919.⁷ Growth of beech and sycamore trees. Carnegie Inst. Wash. Year Book No. 18, 77-78.
- *———. 1920. Course of growth in trees as measured by the dendrograph. Carnegie Inst. Wash. Year Book No. 19, 49-50.
- *———. 1921.¹ Growth in trees. Carnegie Inst. Wash. Pub. No. 307.
- *———. 1921.² Growth in trees. Carnegie Inst. Wash. Year Book No. 20, 44-46.
- *———. 1921.³ The autograph of the Arizona ash tree. Garden, vol. 34, 305.
- *———. 1921.⁴ Growth in trees. Proc. Amer. Philos. Soc., vol. 60, 7-14.
- *———. 1922. Dendrographic records of growth in trees. Carnegie Inst. Wash. Year Book No. 21, 57.
- *———. 1924.¹ Dendrographic measurements (p. 1-88 of D. T. MacDougal and F. Shreve, Growth in trees and massive organs of plants). Carnegie Inst. Wash. Pub. No. 350.
- *———. 1924.² Dendrographic records of growth in trees. Carnegie Inst. Wash. Year Book No. 22, 43-44.
- *———. 1924.³ Growth in trees, recorded by the dendrograph. Carnegie Inst. Wash. Year Book No. 23, 125-126.
- *———. 1924.⁴ Growth in cacti. Carnegie Inst. Wash. Year Book No. 23, 126-127.
- *———. 1925.¹ Reversible variations in volume, pressure and movements of sap in trees. Carnegie Inst. Wash. Pub. No. 365.
- *———. 1925.² Tree trunks, growth and reversible variations in circumference. Science n.s., vol. 61, 370-372.
- *———. 1925.³ Growth in trees. Scien. Month., vol. 21, 99-103.
- *———. 1925.⁴ Accretion and distention in plant cells. Amer. Naturalist, vol. 59, 336-345.
- *———. 1925.⁵ Reversible variations in volume of stems and movement of sap. Carnegie Inst. Wash. Year Book No. 24, 138-139.
- *———. 1926.¹ The hydrostatic system of trees. Carnegie Inst. Wash. Pub. No. 373.
- *———. 1926.² The autobiography of trees. Amer. Forests and Forest Life, vol. 32, 661-662.
- *———. 1927.¹ Factors or agencies affecting growth, especially in trees. Carnegie Inst. Wash. Year Book No. 26, 149-150.
- *———. 1927.² Dendrographic records of a poplar. Carnegie Inst. Wash. Year Book No. 26, 151-152.
- *———. 1927.³ The course of growth in the tree cactus. Carnegie Inst. Wash. Year Book No. 26, 152.
- *———. 1929.¹ Records of tree growth. In Reports of Conferences on Cycles, Carnegie Inst. Wash., 6-7.
- *———. 1929.² Trees as recorders. In Reports of Conferences on Cycles, Carnegie Inst. Wash., 26-34.
- *———. 1930.¹ Continuous and non-rhythmic action of cambium. Carnegie Inst. Wash. Year Book No. 29, 198-199.
- *———. 1930.² Dendrographic measurements. Carnegie Inst. Wash. Year Book No. 29, 199-200.
- *———. 1930.³ Lengthened growth periods in transplants. Carnegie Inst. Wash. Year Book No. 29, 200.
- *———. 1930.⁴ Lengthened growth periods and continuous growth. Proc. Amer. Philos. Soc., vol. 69, 329-345.
- *———. 1931.¹ Scope of dendrographic studies. Carnegie Inst. Wash. Year Book No. 30, 241-242.
- *———. 1931.² Localized activity of cambium. Carnegie Inst. Wash. Year Book No. 30, 242.
- *———. 1931.³ Ratio of wood formed to photosynthetic surface. Carnegie Inst. Wash. Year Book No. 30, 242-243.
- *———. 1932.¹ Growth of the tree-cactus (*Carnegiea gigantea*). Carnegie Inst. Wash. Year Book No. 31, 194-195.
- *———. 1932.² Seasonal action of the redwood (*Sequoia sempervirens*). Carnegie Inst. Wash. Year Book No. 31, 195.
- *———. 1932.³ Reversible variations in diameter of a tree-cactus. Carnegie Inst. Wash. Year Book No. 31, 199-200.
- *———. 1933.¹ The relation of leaf-surface to wood formation in pine trees. Proc. Amer. Philos. Soc., vol. 72, 325-332.

- * MACDOUGAL, D. T. 1933.² Continuous and discontinuous growth of cambium. Carnegie Inst. Wash. Year Book No. 32, 189-190.
- * ———. 1933.² Relation of leaf surface to amount of wood formation. Carnegie Inst. Wash. Year Book No. 32, 188-189.
- . J. B. OVERTON and G. M. SMITH. 1929. The hydrostatic-pneumatic system of certain trees; movements of liquids and gases. Carnegie Inst. Wash. Pub. No. 397.
- * ———, H. VON SCHRENK and F. SHREVE. 1921. History of growth in a Monterey pine, as read from the longitudinal section of the trunk of a full-grown tree. Carnegie Inst. Wash. Year Book No. 20, 70-71.
- , and E. B. WORKING. 1933. The pneumatic system of plants, especially trees. Carnegie Inst. Wash. Pub. No. 441.
- MAGISTAD, O. C., and J. F. BREAZEALE. 1929. Plant and soil relations at and below the wilting percentage. Univ. Arizona Tech. Bul. 25.
- MALLOCK, A. 1919. Growth of trees, with a note on interference bands formed by rays at small angles. Proc. Roy. Soc. London, B., vol. 90, 186-191.
- MEINECKE, E. P. 1925. An effect of drought in the forests of the Sierra Nevada. Phytopathology, vol. 15, 549-553.
- MOINAT, A. D. 1932. Available water and the wilting of plants. Plant Physiology, vol. 7, 35-46.
- MORIKAWA, K. 1925. Über die Beziehungen zwischen dem Streckungs- und dem Dickenwachstum an den Jahrestrieben von *Pinus densiflora* und *P. Thunbergii*. Bul. Sci. de la Fak. Terkultura, Kjusu Imperia Universitato, vol. 1, 292-309 (*Germ. summary, 308-309*).
- MÜNCH, E. 1927. Versuche über den Saftkreislauf. Ber. deutsche bot. Ges., Bd. 45, 340-356.
- NÖRDLINGER, H. 1871. Der Holzring als Grundlage des Baumkörpers, (*Cited by Grossenbacher, 1915*).
- PALLADIN, V. I. 1926. (Livingston, B. E., ed). Plant physiology, 3d Amer. Ed.
- PEARSON, G. A. 1918. The relation between spring precipitation and height growth of western yellow-pine saplings in Arizona. Jour. For., vol. 16, 677-689.
- * ———. 1924. The growing season of western yellow pine. Jour. Agr. Res., vol. 29, 203-204.
- PFEFFER, W. 1903. (Ewart, Alfred J., trans.) The Physiology of Plants, a treatise upon the metabolism and sources of energy in plants. 2d. Ed., vol. II.
- * PHILLIPS, J. F. V. 1927.² Dendrographic experiments: *Ocotea bullata* E. Mey. ("Stinkwood"). S. Afr. Jour. Sci., vol. 24, 227-243 (abstract) (*cited by Phillips, 1931*).
- * ———. 1927.² Growth and regeneration in subtropical forests. Carnegie Inst. Wash. Year Book No. 26, 322-323.
- * ———. 1931. Forest succession and ecology in the Knysna region. Bot. Surv. of South Afr. Mem. 14.
- PRIESTLEY, J. H. 1930. Studies in the physiology of cambial activity. III: The seasonal activity of the cambium. New Phytologist, vol. 29, 316-354.
- ROBBINS, W. J. 1921. Precipitation and the growth of oaks at Columbia, Missouri. Mo. Agr. Exper. Sta. Res. Bul. 44.
- ROMELL, L. G. 1925. Växttidsundersökningar å tall och gran (Study of time of growth in pine and spruce). Meddelanden från Statens Skogsförsöksanstalt, Häft. 22, 45-124.
- SCHIMPER, A. F. W. 1903. (W. R. Fisher, trans.) Plant geography upon a physiological basis.
- SIMON, S. 1914. Studien über die Periodizität der Lebensprozesse der in dauernd feuchten Tropengebieten heimischen Bäume. Jahrb. wiss. Bot., Bd. (i. e. vol.) 54, 71-187. (*Cited by Priestley, 1930*).
- SMITH, F., R. B. DUSTMAN, and C. A. SHULL. 1931. Ascent of sap in plants. Bot. Gaz., vol. 91, 395-410.
- SPALDING, E. S. 1905. Mechanical adjustment of the Sahuaro (*Cereus giganteus*) to varying quantities of stored water. Bull. Torr. Bot. Club, vol. 32, 57-68.
- . 1910. Form-alterations and growth of cacti. In MacDougal, D. T., and E. S. Spalding, The water-balance of succulent plants, Carnegie Inst. Wash. Pub. No. 141.
- STAMM, ALFRED J. 1929. The fiber-saturation point of wood as obtained from electrical conductivity measurements. Indus. and Eng. Chem., Analytic. Ed. vol. 1, No. 2, 94.
- STEWART, O. M. 1924. Physics, a text book for colleges.

- STOCKER, O. 1929. Das Wasserdefizit von Gefäßpflanzen in verschiedenen Klimazonen. *Planta/Archiv für wiss. Bot.*, Bd. 7, 382-387.
- SUDWORTH, G. B. 1927. Check list of the forest trees of the United States, their names and ranges. U. S. Dept. Agr. Misc. Cir. 92.
- TUMANOW, I. I. 1930. Welken und Dürre-resistenz. *Wissenschaftliches Archiv für Landwirtschaft* Bd. (i. e. vol.) 3, 389-419.
- ÚLEHA, VLADIMIR. 1926. The significance of the water deficit in living cells. *Carnegie Inst. Wash. Year Book* No. 25, 167-169.
- VEIHMAYER, F. J. 1927. Some factors affecting the irrigation requirements of deciduous orchards. *Hilgardia*, vol. 2, 125-284.
- WEAVER, J. E., and A. MOGENSEN. 1919. Relative transpiration of coniferous and broad-leaved trees in autumn and winter. *Bot. Gaz.*, vol. 68, 393-424.
- WHITE, W. N. 1932. A method of estimating ground-water supplies based on discharge by plants and evaporation from soil. Results of investigations in Escalante Valley, Utah. U. S. Dept. Int. Geol. Surv. Water-Supply Paper 659-A.
- WILSON, J. D. 1927. The measurement and interpretation of the water-supplying power of the soil with special reference to lawn grasses and some other plants. *Plant Physiology*, vol. 2, 385-440.
- WOODHOUSE, E. D. 1933. Sap hydraulics. *Plant Physiology*, vol. 8, 177-202.